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Úloha hnízda při reprodukci rákosníka velkého

The role of nest in reproduction of the Great Reed Warbler

Disertační práce

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Prohlášení:

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V Praze, Podpis

Poděkování

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Obsah

Předmluva

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Abstrakt

Ptačí hnízda poskytují ochranu vejcím a mláďatům, umožňují rodičům bezpečně opustit potomstvo a zase se k němu vrátit, jejich termoregulační vlastnosti snižují energetické náklady na inkubaci vajec a zahřívání mláďat, a jsou tedy klíčovými strukturami v reprodukci drtivé většiny druhů ptáků. Díky svému významu by tedy měla podléhat přírodnímu výběru. Bylo proto navrženo několik hypotéz, které popisují selekční tlaky, jež na velikost hnízda samého nebo některých jeho částí působí. Ve své dizertační práci jsem testoval platnost několika z nich u rákosníka velkého (*Acrocephalus arundinaceus*) – otevřeně hnízdícího druhu pěvce, jehož hnízda jsou k tomu velmi vhodná, neboť vykazují značnou velikostní variabilitu. K tomuto účelu jsem využil jak rozsáhlého datového souboru několika set změřených hnízd tohoto druhu, tak i experimentů, při kterých jsem s velikostí rákosničích hnízd aktivně manipuloval.

Ve shodě s předchozími studiemi se nám nepodařilo prokázat, že by velikost hnízda rákosníka velkého měla vliv na pravděpodobnost jeho parazitace kukačkou obecnou (*Cuculus canorus*). Ta byla ovšem ovlivněna několika jinými faktory, a to načasováním hnízdění, hustotou rákosového porostu v blízkosti hnízda, a především jeho viditelností z nejbližšího potenciálního místa, ze kterého kukačky hostitelská hnízda vyhledávají. Zároveň jsme ukázali, že kukačky mění svoji strategii při hledání hnízd podle jejich dostupnosti. V době, kdy byl hostitelských hnízd nedostatek, totiž parazitovaly všechna hnízda včetně těch nejlépe ukrytých, zatímco v době, kdy hnízdilo velké množství hostitelských párů, se spíše soustředily na hnízda nápadnější, snadněji nalezitelná (vše **Kapitola 1**). To, zda bylo hnízdo parazitováno kukačkou, mělo vliv i na pravděpodobnost jeho predace ve fázi inkubace (**Kapitola 2**), nejspíše právě z toho důvodu, že si kukačky vybíraly k parazitaci hůře ukrytá hnízda (**Kapitola 1**). Obecně jsou ale hnízda rákosníka velkého predována ve srovnání s ostatními druhy evropských pěvců mnohem vzácněji. Pravděpodobnost, že přežijí fázi inkubace, dosahovala na naší studijní lokalitě vysokých 88 až 94 % právě v závislosti na tom, zda hnízdo bylo parazitováno, nebo ne (**Kapitola 2**). Možná i díky takto nízkému predačnímu tlaku jsme v pokusu s umělými hnízdy nezaznamenali, že by jejich velikost významně ovlivňovala pravděpodobnost jejich predace. Pouze aktivní hnízda, experimentálně zvětšená na velikost odpovídající horní hranici přirozené velikostní variability, byla predována marginálně nesignifikantně častěji než mnohem menší hnízda kontrolní (vše **Kapitola 3**). Samci, jimž byla hnízda takto zvětšena, zvýšili svou aktivitu během krmení a nosili mláďatům více potravy než samci z kontrolních hnízd, zatímco samice krmily mláďata se stejným úsilím u obou typů hnízd. Protože hnízda rákosníka velkého jsou stavěna výhradně samicemi, ukazuje tento výsledek na to, že by u tohoto druhu mohla velikost hnízda fungovat jako postkopulační signál kvality samice. Kvalitnější samice by v tomto případě stavěly větší hnízda, na což by samci reagovali zvýšením svého reprodukčního úsilí. Tomu nasvědčuje i analýza velkého vzorku nemanipulovaných hnízd, kdy do větších hnízd bylo snášeno i signifikantně více vajec a bylo z nich vyváděno i více mláďat (vše **Kapitola 4**). Velikost snůšky by ale spíše než s velikostí celého hnízda měla především souviset s velikostí hnízdní kotlinky, jejíž rozměry by měly odpovídat počtu snesených vajec. Tento vztah se ovšem u rákosníka velkého podařilo prokázat pouze u hloubky kotlinky, ale nikoliv pro její šířku. Oba rozměry byly zároveň ovlivněny i velikostí samice, kdy větší samice stavěly i větší kotlinky. Rozměry kotlinek stavěných stejnými samicemi během jedné hnízdní sezony se ovšem signifikantně lišily – náhradní hnízda měla kotlinky menší (mělčí i užší), což korespondovalo i s rozdíly mezi prvními a náhradními hnízdy v jejich celkové velikosti a počtu vajec. To nasvědčuje tomu, že by samice rákosníka velkého mohly rozměry svých hnízdních kotlinek přizpůsobovat očekávané velikosti snůšky, ačkoliv robustní analýza například většího počtu hnízd stavěných stejnými jedinci v různých hnízdních sezonách bohužel stále chybí (vše **Rukopis 5**).

Abstract

Bird nests protect eggs and nestlings, allowing the parents to leave their offspring and subsequently return to them. Their thermoregulatory properties reduce energetic costs of incubation and brooding of nestlings. For all these reasons, nests are key structures for the reproduction of a majority of avian species and as such they should be subject to natural selection. Several hypotheses describing selection pressures which affect the size of nests or some of their parts have been suggested. In my PhD thesis, I investigated some of them in the great reed warbler (*Acrocephalus arundinaceus*) – an open nesting passerine species with very variable nest size. For this purpose, I used a large dataset of several hundred measured great reed warbler nests, nest enlargement experiments and an experiment with artificial nests.

In accordance with previous studies, we did not find that nest size affects the probability of common cuckoo (*Cuculus canorus*) brood parasitism, while it was influenced by other factors, such as timing of breeding, reed density around the nest and nest visibility from the nearest potential cuckoo perch site. More interestingly, we found that cuckoos adjust their nest-searching strategy in relation to availability of host nests. When host nests were scarce, cuckoos parasitized all of them regardless of their concealment; however, when many host pairs bred simultaneously, they chose rather more conspicuous and visible nests (all in **Chapter 1**).

We also found that brood parasitism was an important predictor of nest predation in the incubation stage of the nesting cycle (**Chapter 2**) probably because cuckoos more likely parasitized less concealed nests (**Chapter 1**) even though great reed warbler nests rank among the least predated European passerines. The probability of surviving the incubation stage was 88% or 94% in relation to brood parasitism, with lower nest survival in parasitized nests (**Chapter 2**).

Maybe due to such a low predation pressure we did not find that the probability of survival of artificial experimental nests was significantly influenced by its size. Only active natural nests experimentally enlarged to the size of the largest great reed warbler nests were depredated marginally non-significantly more often than the much smaller non-manipulated controls (all in **Chapter 3**). Males with such enlarged nests brought more food to their offspring than those in control nests, while females fed their nestlings similarly in both treatments. As great reed warbler nests are built exclusively by females, this result suggests that nest size could serve as a signal of female quality. Accordingly, higher quality females should build larger nests which should stimulate males to increase their parental investment. This possibility is supported also by the analysis of an extensive dataset of non-manipulated great reed warbler nests where larger nests contained larger clutches and produced more fledglings (all in **Chapter 4**).

Clutch size should be primarily related to the size of the nest cup, dimensions of which should correspond to the number of laid eggs to ensure the best conditions for incubation and sufficient space for the whole brood of nestlings. Nonetheless, we found such a relationship only in nest cup depth but not in nest cup width, while both nest cup dimensions were influenced by the size of the female as larger females built larger nest cups. However, the same females did not always build nest cups of the same size, because nest cups in replacement nests were smaller than nest cups in first nests in both their dimensions which corresponded to the change in external nest size as well as in the clutch size. These results suggest that great reed warbler females could adjust nest cup size to the intended clutch size. Unfortunately, a robust analysis which would resolve this problem by using a sufficient sample of nests built by the same female in different breeding seasons is still missing (all in **Chapter 5**).

Úvod

Reprodukční úspěch ptáků závisí na mnoha faktorech. Pokud vynecháme často opomíjené štěstí, jedná se především o kvalitu partnera, hnízdního teritoria, umístění hnízda a v neposlední řadě také o kvalitu hnízda samého. Mezi nejdůležitější funkce hnízda spojené s rozmnožováním patří poskytování opory vejcím a následně i rostoucím mláďatům, a snižování energetických výdajů rodičů během inkubace vajec a zahřívání mláďat. Hnízdo zároveň do určité míry chrání svůj obsah před nepříznivými vlivy okolního prostředí, a umožňuje tak rodičům bezpečně opustit potomstvo a zase se k němu vrátit (Hansell 2000). Význam hnízda pro reprodukci není ovšem u všech ptačích druhů stejný. Největší je u altriciálních druhů, u kterých na hnízdě probíhá nejen inkubace vajec, ale i většina péče o mláďata před jejich osamostatněním. Význam hnízda v regulaci energetických výdajů na inkubaci roste i se snižující se velikostí ptačího druhu, neboť čím je druh menší, tím zabírá jeho snůška relativně větší část hnízdní nažiny inkubujících ptáků (Deeming 2013). Obsah hnízda, ať jsou to vejce, nebo mláďata, je vystaven nejen rozmarům počasí, ale i vlivu predátorů, případně hnízdních parazitů či ektoparazitů. Vlastnosti hnízd tak mohou být důležité i v boji proti nim.

Ptačí hnízda vykazují vysokou míru velikostní, tvarové i materiálové diverzity. Tato diverzita je obzvlášť patrná u hnízd pěvců, kteří tvoří více než polovinu všech ptačích druhů, a podílejí se tak i největší měrou na diverzitě ptačích hnízd. I v avifauně České republiky obsahující pouze asi 190 pravidelně hnízdících druhů (Šťastný a Hudec 2011) můžeme najít druhy stavějící hnízda všech čtyř základních typů – otevřená hnízda pěnic, uzavřená hnízda budníčků, hnízda umístěná na zemi, která staví například skřivanovití, a hnízda umístěná v dutinách, jež staví sýkory nebo lejsci (Hansell 2000). Tato hnízda zároveň vynikají i velkou materiálovou různorodostí. Nalezneme mezi nimi hnízda, k jejichž stavbě byly použity různé typy rostlinného materiálu - větvičky, stonky bylin, stébla trav, kůra, mech, stélky lišejníků, ale i bláto, srst či peří (Šťastný a Hudec 2011). Poměrně značnou variabilitu lze ovšem najít i u hnízd jednoho ptačího druhu, kde se jednotlivá hnízda mohou lišit především svou velikostí (např. Schleicher *et al.* 1996, Walsh *et al.* 2010, obr. str. 65 a 66), a to ať svými vnějšími rozměry, nebo rozměry hnízdní kotlinky.

Ve své dizertační práci se zabývám hnízdy rákosníka velkého (*Acrocephalus arundinaceus*). Ta jsou stavěna převážně z rostlinného materiálu, stonků a listů rákosu, trav a dalších podobných rostlin (Kožená-Toušková 1973), s občasnou příměsí exotičtějších materiálů, jakými jsou hadí svlečky, které rákosník dokonce aktivně vyhledává (Trnka a Prokop 2011), řasy, peří, vzácně pak i pozůstatky po lidské činnosti, například různé provázky, kousky igelitu a podobně (vlastní pozorování, obr. str. 65). Obecně jsou však hnízda tohoto druhu až na občasné výjimky materiálově značně uniformní, a proto se v předkládané dizertační práci dále zabývám pouze jejich velikostí, která se u tohoto druhu může značně lišit (obr. str. 66). Hlavním cílem této dizertační práce proto bylo popsat velikostní variabilitu hnízd rákosníka velkého a zjistit, jakou roli hraje tato variabilita při jeho reprodukci.

Na velikost hnízda by totiž mělo, či spíše mohlo, mít vliv několik navzájem protichůdně působících selekčních tlaků. Některé by měly vést ke zmenšování hnízda, případně pouze jeho určitých částí (např. hnízdní kotlinky), jiné naopak spíše k jeho zvětšování. Predace a hnízdní parazitismus by měly zvýhodňovat menší hnízda, která budou mít menší šanci, že je predátoři nebo hnízdní parazité najdou (Møller 1990a, Palomino *et al.* 1998, Moskát a Honza 2000). Hnízda s tlustšími stěnami by měla lépe izolovat obsah hnízda od okolního prostředí, a snižovat tak energetické nároky na inkubaci (Palomino *et al.* 1998). Větší hnízdní kotlinka lépe pojme větší počet mláďat, a nebude tak hrozit, že by některé z nich mohlo vypadnout (Slagsvold 1982). Hnízda s kvalitnějšími a masivnějšími elementy, které je připevňují k podkladu, by měla být stabilnější, snižující riziko převrhnutí a vysypání vajec či mláďat (Collias a Collias 1984). Velikost hnízda by také mohla fungovat jako postkopulační signál mezi partnery, kdy by větší aktivita jednoho z nich během stavby měla odrážet jeho kvalitu, případně ochotu investovat do další reprodukce, na což by druhý z partnerů měl reagovat zvýšením svého reprodukčního

úsilí například během krmení či obraně hnízda před predátory a hnízdními parazity (Moreno *et al.* 1994, Soler *et al.* 1998a).

Rákosník velký je ideální druh pro testování všech těchto předpokladů. Je to středně velký druh pěvce dosahující v hnízdní době hmotnosti přibližně 30 g (Leisler 1991, Cramp 1992). Staví si otevřená miskovitá hnízda horizontálně připevněná k několika stéblům rákosu obecného (*Phragmites australis*) či stonkům orobince úzkolistého (*Typha angustifolia*). Svá hnízda nevyužívá opakovaně. To znamená, že pokud je hnízdo například vypleněno predátorem a oba členové páru se rozhodnou pro náhradní hnízdění, je pro tento hnízdní pokus postaveno v naprosté většině případů hnízdo úplně nové (stejné hnízdo bylo po úpravě hnízdní kotlinky opětovně použito pouze při třech náhradních hnízděních z 255, data z let 2008-2015). To dělá z rákosníka velkého ideální druh pro studium vlastností hnízda, ať se jedná o jejich velikost nebo umístění v prostředí. Díky tomu jsem se mohl ve své dizertační práci pokusit odpovědět na tyto konkrétní otázky:

1) Ovlivňuje velikost hnízda rákosníka velkého pravděpodobnost parazitace kukačkou obecnou (*Cuculus canorus*)? (**Kapitola 1**)
2) Jaké je přežívání hnízd rákosníka velkého (**Kapitola 2**) a je ovlivněno velikostí hnízda? (**Kapitola 3**)
3) Signalizuje velikost hnízda rákosníka velkého kvalitu partnera a míru jeho ochoty podílet se na další reprodukci, a funguje tedy jako signál mezi partnery? (**Kapitola 4**)
4) Přizpůsobuje samice rákosníka velkého velikost hnízdní kotlinky velikosti své snůšky? (**Kapitola 5**)

Hnízdo a parazitace

Na lokalitě Hodonínských a Mutěnických rybníků, kde probíhala veškerá terénní část výzkumu, jehož výsledky jsou prezentovány v této dizertační práci, dosahuje hnízdní populace rákosníka velkého poměrně značné početnosti. Ta se v letech 2008 – 2015 pohybovala mezi 73 a 108 hnízdícími samicemi, které během svých hnízdních pokusů postavily celkem 109 až 166 hnízd ročně. Z těchto dat je zřejmé, že vysoké procento samic započne každý rok více než jeden hnízdní pokus a že je tedy poměrně značný počet hnízdění neúspěšných. Největším zdrojem tohoto hnízdního neúspěchu je hnízdní parazitismus kukačkou obecnou (Tab. 1).

Tabulka 1: Příčiny hnízdního neúspěchu hnízd rákosníka velkého na studijní lokalitě Mutěnické a Hodonínské rybníky v letech 2008-2015.

Úspěšná hnízda	472
Neúspěšná hnízda	
Parazitace*	247
Predace	155
Jiné přirozené	110
Výzkum	39
Neurčitelné	18
Celkem	1041

* z toho 36 mláďat kukaček bylo predováno

Kukačka obecná (dále jen „kukačka“) je obligátní hnízdní parazit, a přenechává tedy veškerou péči o své potomstvo svým hostitelům. V případě, že hostitelé parazitické vejce neodmítnou (ať již jeho vyhozením, nebo opuštěním celého hnízda), vytlačí kukaččí mládě během prvních dnů po vylíhnutí

z hnízda všechna zbývající vejce, případně mláďata, čímž si usurpuje veškerou rodičovskou péči svých hostitelů (Wyllie 1981, Davies 2000). Úspěšná parazitace kukačkou má tedy pro hostitele ještě horší důsledky než predace hnízda, neboť ta jim alespoň dovoluje prakticky vzápětí začít náhradní hnízdění. Reprodukční úspěch hostitelů je tak díky parazitaci nejen nulový, ale ještě se navíc vyčerpají nákladnou péčí o mládě parazita. Hostitelé by se proto měli maximálně snažit snížit riziko, že budou parazitováni. Z tohoto důvodu je právě vztah mezi hnízdními parazity a jejich hostiteli velmi intenzivně studován a stal se základním modelovým systémem při výzkumu koevoluce (Rothstein 1990).

Kukačka na studijní lokalitě parazituje všechny čtyři zde hnízdící druhy rákosníků. Rákosník zpěvný (*Acrocephalus palustris*) a rákosník proužkovaný (*Acrocephalus schoenobaenus*) jsou parazitováni spíše vzácně, zatímco rákosník obecný (*Acrocephalus scirpaceus*) je relativně běžným hostitelem (míra parazitace 5 – 20 %, data z let 2010 až 2015). Nejčastějším hostitelem kukačky je pak právě rákosník velký, u něhož dosahovala maximální míra parazitace mezi roky 2008 a 2015 až 68 % ročně. Je tedy zřejmé, že pro rákosníky velké i všechny ostatní hostitelské druhy představuje vyhnutí se parazitaci velkou výhodu. V průběhu let byla proto značná pozornost věnována právě identifikaci podnětů, které kukačky používají při hledání hostitelských hnízd, a snaze zjistit, které vlastnosti hnízdního místa, hnízda či hostitelů samotných ovlivňují to, zda se hostitelé parazitaci vyhnou, nebo ne (Feeney *et al.* 2012). A právě rákosník velký byl v této souvislosti často zkoumaným druhem (Moskát a Honza 2000, Avilés *et al.* 2009, Honza *et al.* 2014, **Kapitola 1**).

Samice kukaček vyhledávají hnízda vhodná k parazitaci již v době jejich stavby podle aktivity hostitelů tak, že je nenápadně pozorují z blízkého vyvýšeného místa, nejčastěji stromu, případně drátu či sloupu elektrického vedení (Wyllie 1981, Honza *et al.* 2002). Větší šanci vyhnout se parazitaci mají proto hnízda umístěná dále od tohoto nejbližšího pozorovacího místa (Alvarez 1993, Øien *et al.* 1996, Moskát & Honza 2000, Antonov *et al.* 2006, Antonov *et al.* 2007, ale ne **Kapitola 1**) a hnízda lépe ukrytá v okolní vegetaci (Øien *et al.* 1996, Moskát a Honza 2000, Clarke *et al.* 2001, Avilés *et al.* 2009, **Kapitola 1**) – pro kukačku tedy hůře viditelná (Moskát a Honza 2000, **Kapitola 1**). Viditelnost hnízda v prostředí by se měla zvětšovat i s jeho velikostí a kukačky by díky tomu měly spíše či snadněji objevit právě hnízda větší (Moskát a Honza 2000). To se ovšem zatím nikomu prokázat nepodařilo (Palomino *et al.* 1998, Moskát a Honza 2000, Antonov *et al.* 2007, Avilés *et al.* 2009, **Kapitola 1**), a to ani v pokusu, kdy byla aktivní hostitelská hnízda zvětšena před začátkem snášení prakticky na dvojnásobek (**Kapitola 3**). Stejně tak nebylo prokázáno, že by k ochraně hnízda před parazitací přímo přispívala míra agresivity hostitelského páru (Welbergen and Davies 2009, **Kapitola 1)**, ačkoliv například rákosník velký, u něhož byl vliv agresivity na pravděpodobnost parazitace kukačkou také testován (**Kapitola 1**), je druhem velmi agresivním, který běžně na kukačku útočí pomocí kontaktních ataků (Požgayová *et al.* 2009) a který je schopen ji během parazitace dokonce i zabít (Molnár 1944, Janisch 1948-1951, Mérő a Žuljević 2014).

Mohlo by se tedy zdát, že by rákosníkům mohlo stačit postavit si hnízda v teritoriích daleko od stromů, která jsou navíc zarostlá velmi hustým rákosovým porostem, a měli by nad kukačkami vyhráno. Takových teritorií je ovšem obvykle velmi málo a jen málo rákosníků má to privilegium v nich hnízdit. Tato teritoria nemusí být navíc ani vhodná, co se týče například potravní nabídky. Na druhou stranu je pro kukačky, stejně jako pro všechny obligátní hnízdní parazity, schopnost nalézt hostitelské hnízdo naprosto zásadní součástí reprodukce. Mnohem zásadnější, než je pro rákosníky snaha vyhnout se parazitaci. Kukačky totiž, aby se rozmnožily, hostitelská hnízda najít musí, zatímco hostitelé parazitování být vůbec nemusí a často se rozmnoží, i když parazitováni jsou (parazitické vejce odmítnou, nevylíhne se apod.). Schopnost vyhnout se parazitaci tak pro ně většinou představuje „pouze“ konkurenční výhodu. Selekce na schopnost kukaččích samic nalézt dostatek vhodných hostitelských hnízd je proto určitě velmi silná. Dalo by se tedy očekávat, že kukačky budou schopné nalézt i mnohá prakticky dokonale ukrytá hostitelská hnízda, což se také často i děje (**Kapitola 1**). Zároveň by se kukaččí samice měly snažit maximalizovat svůj reprodukční úspěch, a parazitovat tedy co největší počet hostitelských hnízd.

Pravděpodobnost, že bude hostitelské hnízdo parazitováno, musí být také závislá na populačních hustotách jak hnízdních parazitů, tak i jejich hostitelů. Čím je parazitů méně, tím bude pravděpodobnost parazitace hostitelského hnízda menší a naopak. Dále platí, že pravděpodobnost parazitace daného hnízda bude tím nižší, čím více hostitelských párů bude hnízdit současně (Clark a Robertson 1979). Hnízdní parazité totiž mají pouze omezený časový úsek, během něhož mohou hostitelské hnízdo parazitovat (Davies 2000), a některá hostitelská hnízda se tak vyhnou parazitaci prostým vlivem náhody (Clark a Robertson 1979, Martínez *et al.* 1996, **Kapitola 1**). Hnízdní parazité pak mohou na dostupnost hostitelských hnízd reagovat i změnou strategie jejich vyhledávání, a to takovým způsobem, aby měli co největší šanci najít a následně parazitovat maximální počet hostitelů. To se nám podařilo prokázat právě u kukačky. Samice kukaček totiž v době nedostatku hnízd rákosníka velkého parazitovaly všechna hnízda, včetně těch velmi dobře ukrytých, zatímco v době jejich nadbytku se soustředily spíše na ta hůře ukrytá, která jim pravděpodobně nedalo takovou práci nalézt (**Kapitola 1**).

Hnízdo a predace

Predace je hlavním zdrojem mortality většiny druhů ptáků (Martin 1995) a predace hnízd pak i hlavním zdrojem jejich hnízdního neúspěchu (Ricklefs 1969, Martin 1993). Je proto celkem překvapující, že studií, ve kterých by se autoři snažili určit míru mortality hnízd jednotlivých druhů způsobenou predátory, není příliš mnoho. Dobře je to vidět právě na rákosníkovi velkém, druhu velmi intenzivně studovaném, u něhož byly v rámci různých vědeckých projektů nalezeny stovky až tisíce hnízd (např. Bensch 1996, Moskát a Honza 2000, Dyrcz a Halupka 2009, Avilés *et al.* 2009, Mérő *et al.* 2015). Pokud nějaké predační studie existují, jsou často poměrně letité a míra predace hnízd u nich bývá ukryta v celkové hnízdní úspěšnosti (Havlín 1971, Dyrcz 1980, Bensch a Hasselquist 1994, Mérő *et al.* 2015) nebo v úspěšnosti vajec (Petro *et al.* 1998), společně se všemi ostatními příčinami hnízdní mortality. Přesto se u většiny těchto studií dá po jejich více či méně pečlivém prostudování určit alespoň podíl predovaných hnízd z jejich celkového počtu (Tab. 2). Ten se pohybuje od 12,1 do 52 %, a pokud nebudeme brát v úvahu studie s velmi malým až nedostatečným počtem nalezených hnízd (Bátary a Báldi 2005, Trnka *et al.* 2009), pak činí podíl predovaných hnízd 12,1 až 41,6 % (Tab. 2).

Výše popsaný postup výpočtu hnízdní úspěšnosti (poměr neúspěšných hnízd k jejich celkovému počtu), tedy tzv. tradiční metoda (Weidinger 2003), je sice intuitivní, jednoduchá a běžně používaná, umožňující získat základní představu o míře přežívání hnízd, potažmo míře jejich predace, její velkou nevýhodou ale je, že skutečnou hnízdní úspěšnost značně nadhodnocuje (Weidinger 2003). Je tomu tak především proto, že úspěšná hnízda mají již z definice větší šanci být nalezena (např. díky vyplašení inkubujícího jedince, viz Praus a Weidinger 2015), zatímco část neúspěšných hnízd nebude nalezena nikdy (Miller a Johnson 1978, Weidinger 2003). Z tohoto důvodu převažuje v současné době ve studiích analyzujících hnízdní úspěšnost tzv. Mayfieldova metoda (Mayfield 1961, 1975), která poskytuje korektnější odhady hnízdní úspěšnosti.

Mayfieldova metoda je založena na výpočtu tzv. denní míry přežívání („daily survival rate" - DSR) – pravděpodobnosti, s jakou se hnízdo dožije dalšího dne. Podobným způsobem jako DSR je možné vypočítat i denní míru predace („daily predation rate" - DPR) určující pravděpodobnost, že bude hnízdo do dalšího dne vypleněno predátorem. Pokročilejší metody statistické analýzy založené na DSR pak umožňují odpovídat i na komplikovanější otázky, například zjišťovat vliv dalších proměnných na hnízdní úspěšnost. Nejčastěji se jedná o proměnné prostředí týkající se hnízdního místa (např. Hannon *et al.* 2009, Praus a Weidinger 2015) či jeho širšího okolí (Pasinelli a Schiegg 2006, Baláž *et al.* 2007), věk mláďat (**Kapitola 2**, Musilová *et al.* 2014), obsah hnízda (**Kapitola 2**, Burhans *et al.* 2002), načasování hnízdění (Stumpf *et al.* 2012) apod. (podrobně viz Weidinger 2003). Studie využívající Mayfieldovu metodu a výpočet DSR tak přináší velmi zajímavé výsledky. Určitou nevýhodu ovšem představuje

Tabulka 2: Tabulka sumarizující základní výsledky studií zabývajících se hnízdní úspěšnosti rákosníka velkého. Pro každou studii je hnízd a jejich procentuální zastoupení v dané fázi hnízdění. Predovaná hnízda jsou podmnožinou hnízd neúspěšných.

Studie	Lokalita (stát)	Fáze vajec					Fáze	
		Počet hnízd	Neúspěšná hnízda	%	Predovaná hnízda	%	Počet hnízd	Neúspěšná hnízda
Havlín (1971)*	Náměšťské rybníky (CZ)	182	44	24,2%	30	16,5%	133	8
Dyrcz (1980)	Milicz (PL)	–	–	–	–	–	–	–
Dyrcz (1980)	Lac de Neuchatel, Bielersee (CH)	–	–	–	–	–	–	–
Bensch a Hasselquist (1994)	Jezero Kvismaren (SE)	–	78	–	–	–	–	43
Petro *et al.* (1998)	Heřmanický stav (CZ)	107	–	–	8	7,5%	–	–
Hansson *et al.* (2000)	Jezero Kvismaren (SE)	–	–	–	26	–	–	–
Bátary a Báldi (2005)	Jezero Velence (HU)	25	–	–	6	24,0%	–	–
Trnka *et al.* (2009)	Trnava (SK)	–	–	–	–	–	–	–
Mérö *et al.* (2015)	Severovýchod Vojvodiny (RS)	–	–	–	–	–	–	–
Rukopis 2[A]	Mutěnické a Hodonínské rybníky (CZ)	793	–	–	74	9,3%	678	–

Stidie[A] uvažuje místo celé fáze vajec pouze fázi inkubace.

Tabulka 3: Tabulka základních výsledků studií, zabývajících se predací a hnízdní úspěšností některých druhů evropských pěvců. Pro rákosníka ostatní druhy se jedná o náhodně vybrané studie ze střední Evropy. Hodnoty DSR a DPR je možné mezi studiemi porovnávat pouze orientačně.

Studie	Druh	Fáze vajec							
		Počet hnízd	Počet hnízdodnů	Neúspěšná hnízda	DSR	Predovaná hnízda	DPR	Počet hnízd	Počet hnízdodnů
Bensch a Hasselquist (1994) ‡[C]	Rákosník velký	–	2230	41	–	–	0,017 - 0,023	–	1444
Trnka *et al.* (2009) ‡	Rákosník velký	–	–	–	–	–	–	–	–
Rukopis 2‡[C]	Rákosník velký	793	8322**	–	–	74	0,005 - 0,011	–	–
Bibby and Thomas (1985)[A]	Rákosník obecný	154	1924	38	0,980	–	–	113	1395
Halupka *et al.* (2014)[C]	Rákosník obecný	–	4712	–	–	–	0,016	–	3033
Rukopis 2‡[C]	Rákosník obecný	723	6032**	–	–	–	0,016 - 0,026	–	–
Neto a Gosler (2005)[AC]	Cvrčilka slavíková	–	–	–	0,979	–	–	–	–
Musilová *et al.* (2014)[A]	Strnad rákosní	–	–	–	–	–	–	–	–
Weidinger (2000)[A]	Pěnice černohlavá	297	2454	142	0,953*	91	–	205	1183
Weidinger (2006)[A]	Pěnice černohlavá	–	–	–	–	–	–	–	–
Baláž *et al.* (2007)[A]	Pěnice černohlavá	–	1077	–	0,977*	–	–	–	609
Weidinger (2006)[A]	Kos černý	–	–	–	–	–	–	–	–
Weidinger (2006)[A]	Drozd zpěvný	–	–	–	–	–	–	–	–
Weidinger (2006)[A]	Strnad obecný	–	–	–	–	–	–	–	–
Praus *et al.* (2014)[A]	Skřivan polní	21	91	5	0,945	4	0,044	53	259
Praus *et al.* (2014)[A]	Skřivan lesní	9	88	5	0,943	5	0,057	34	123

Studie[A] používají s vysokou pravděpodobností k výpočtu DSR modely s konstantních přežíváním po celou dobu dané fáze hnízdění. inkubace a prezentované hodnoty se týkají pouze fáze inkubace. * Průměrné hodnoty DSR vážené počtem hnízdodnů. ‡Hodnoty DSR, případně časových intervalů během nichž došlo k predaci.

zaznamenán počet nalezených hnízd, neúspěšných a predovaných

mláďat		Celé hnízdění				
Predovaná hnízda	%	Počet hnízd	Neúspěšná hnízda	%	Predovaná hnízda	%
2	1,5%	177	52	29,4%	32	18,1%
–	–	322	144	44,7%	96	29,8%
–	–	86	20	23,3%	17	19,8%
–	–	279	121	43,4%	102	36,6%
5	–	107	–	–	13	12,1%
21	–	113	47	41,6%	47	41,6%
7	–	25	14	56,0%	13	52,0%
–	–	45	9	20,0%	9	20,0%
–	–	174	75	43,1%	–	–
47	6,9%	817	–	–	121	14,8%

velkého, rákosníka obecného, cvrčilku slavíkovou a strnada rákosního se jedná o výsledky všech mně známých studií, pro

Fáze mláďat				Celé hnízdění					
Neúspěšná hnízda	DSR	Predovaná hnízda	DPR	Počet hnízd	Počet hnízdodnů	Neúspěšná hnízda	DSR	Predovaná hnízda	DPR
43	–	–	0,026 - 0,034	279	5274	121	–	102	–
–	–	–	–	45	–	9	0,982 - 0,971	9	0,018 - 0,029
–	–	–	–	–	–	–	–	–	–
30	0,978	–	–	–	–	–	–	–	–
–	–	–	0,037	524	–	280	–	215	–
–	–	–	–	–	–	–	–	–	–
–	0,958	–	–	93	–	35	0,970	32	–
–	–	–	–	81	–	–	0,970	–	–
51	0,952*	40	–	502	3637	193	0,947*	131	–
–	–	–	–	340	2804	229	0,918	–	–
–	0,966*	–	–	126	1687	48	0,973*	34	–
–	–	–	–	98	903	67	0,926	–	–
–	–	–	–	81	780	54	0,931	–	–
–	–	–	–	56	427	43	0,899	–	–
12	0,954	9	0,035	58	350	17	0,951	13	0,037
8	0,935	7	0,057	40	211	13	0,938	12	0,057

Studie[B] uvažují pouze predační mortalitu a DSR pro ně proto není uvedena. Studie[C] rozdělují fázi vajec na fázi snášení a fázi DPR jsou odečteny z grafů prezentovaných v těchto studiích. ** Efektivní velikosti vzorku - počet hnízdodnů plus počet

to, že i přes svou sofistikovanost a mnohdy i nespornou kvalitu neposkytují tyto studie základní navzájem porovnatelné hodnoty DSR, neboť metodika výpočtu DSR se mezi nimi, vzhledem k jejich zaměření na určitou a často dosti specializovanou problematiku, značně liší.

Tímto problémem trpí i většina prací využívajících pro studium hnízdní úspěšnosti rákosníka velkého Mayfieldovu metodu. Ty, pokud je mi známo, existují v současné době pouze čtyři (**Kapitola 2**, Bensch a Hasselquist 1994, Bátary a Báldi 2005, Trnka *et al.* 2009), ale žádná z nich neposkytuje konkrétní údaje o DSR či DPR. Jediným řešením je tak alespoň odečet přibližných hodnot DSR/DPR z prezentovaných grafů, což v případě studie Bátaryho a Báldiho (2005), kvůli nevhodné až chybné konstrukci grafu, ani není možné. I ve třech zbývajících studiích (**Kapitola 2**, Bensch a Hasselquist 1994, Trnka *et al.* 2009) je třeba brát hodnoty odečtené z grafů velmi obezřetně. Ve dvou případech je totiž při statistické analýze uvažována pouze predační mortalita, což je způsobeno příliš malým vzorkem hnízd v případě Trnky *et al.* (2009) a použitou metodikou v případě **Kapitoly 2.** Proto je v obou případech lepší mluvit o hodnotách DPR (v tomto případě DPR = 1 – DSR), což je i vhodnější z hlediska zaměření této kapitoly právě na predaci. Trnka *et al.* (2009) zároveň nejasně specifikovali metodiku, jakou byly hodnoty DPR (DSR) vypočítány (délka expozice u predovaných hnízd). V práci Bensche a Hasselquista (1994) a **Kapitole 2** jsou pak hodnoty DSR/DPR získány z modelů, které obsahují větší množství vysvětlujících proměnných. I přes tato omezení se ale zdá, že hodnoty DPR jsou u rákosníka velkého velmi nízké. V případě studie Trnky *et al.* (2009) je to od 0,018 pro hnízda postavená v rákosí po 0,029 pro hnízda v orobinci. **Kapitola 2** pak uvádí hodnoty DPR pro jednotlivé fáze hnízdění zvlášť. Pro fázi inkubace se pohybují mezi 0,005 pro neparazitovaná a 0,011 pro parazitovaná hnízda. Ve fázi mláďat pak pravděpodobnost predace rostla s jejich věkem z 0,008 pro právě vylíhlá mláďata po 0,037 pro mláďata stará osm dní. Pravděpodobnost, že hnízdo bude predováno během 12 dní inkubace tak činí přibližně pouhých 6 – 12 % (vše **Kapitola 2**). Téměř dvojnásobnou pravděpodobnost hnízdního neúspěchu ve fázi inkubace – 18,5 – 24,0 % (DSR = 0,983 – 0,977 v závislosti na statusu hnízda: monogamní, primární, či sekundární) pak udává Bensch a Hasselquist (1994). Ti ovšem ve svých analýzách uvažují všechny příčiny hnízdního neúspěchu dohromady, a proto nejsou jejich výsledky a výsledky v **Kapitole 2** přímo srovnatelné. Počet neúspěšných hnízd z důvodu nepredační mortality (např. opuštění hnízda rodiči kvůli počasí) je ale ve studii Bensche a Hasselquista (1994) poměrně nízký (pouze 15,7 %). Výsledky obou studií by se tudíž v případě shodného způsobu výpočtu DPR pravděpodobně příliš nelišily. Pro fázi mláďat se pak hodnoty DSR pohybují v rozmezí 0,974 až 0,966 opět v závislosti na statusu hnízda (Bensch a Hasselquist 1994).

I přes interpretační komplikace způsobené rozdílnou metodikou sběru dat a statistickou analýzou tak odhady míry predace vypočtené tradiční i Mayfieldovou metodou ukazují, že rákosník velký patří k nejméně predovaným druhům evropských pěvců vůbec (Tab. 3). Jedním z důvodů může být to, že k hnízdění využívá velmi specifický biotop – rákosiny, ve kterém může být predační tlak obecně nižší (viz Tab. 3), a to ještě především porosty rostoucí ve větší hloubce, tedy dál od břehu (Leisler 1981, Graveland 1998). Druhým důvodem pak může být jeho vysoká agresivita (Požgayová *et al.* 2009, **Kapitola 1**), a tedy potenciální schopnost alespoň některé predátory od hnízda odehnat. Příbuzné druhy jako rákosník obecný a druhy hnízdící v podobném prostředí, jako cvrčilka slavíková (*Locustella luscinioides*) a strnad rákosní (*Emberiza schoeniclus*), ani zdaleka nevykazují takovou míru agresivity (Čapek *et al.* 2010, data dostupná pouze pro rákosníka obecného) a zároveň hnízdí v sušších biotopech mnohem lépe dostupných pro suchozemské druhy predátorů (Cramp 1992). Přesto i tyto druhy vykazují mnohem nižší hodnoty DSR než druhy hnízdící v lese a křovinatých biotopech jako například kos černý (*Turdus merula*) či pěnice černohlavá (*Sylvia atricapilla*, Tab. 3). Samostatnou kapitolou jsou pak druhy hnízdící na zemi v otevřených biotopech s extrémně nízkou DSR (např. Praus *et al.* 2014, Praus a Weidinger 2015).

Ačkoliv predace hnízd rákosníka velkého není tak častá jako u jiných druhů, jedná se stále o velmi důležitý zdroj hnízdní mortality (Tab. 1). Přesto nebylo doposud publikováno příliš mnoho studií,

které by se snažily určit faktory ovlivňující pravděpodobnost predace reálných aktivních hnízd tohoto druhu. Ke zjištění míry hnízdní predace tak bylo častěji využíváno pokusů s umělými hnízdy, které mají ale nižší vypovídací hodnotu a jejich výsledky mohou být s výsledky získanými u aktivních reálných hnízd srovnávány jen v omezené míře (Burke *et al.* 2004, Faaborg 2010, McKinnon *et al.* 2010). Některé studie ovšem využívaly oba metodické přístupy zároveň. Například Trnka *et al.* (2009) porovnávali přežívání aktivních i umělých hnízd rákosníka velkého umístěných v rákosí a v orobinci. Statisticky významný rozdíl v DSR mezi těmito dvěma typy prostředí ovšem zaznamenali pouze u hnízd umělých. Umělá hnízda byla také častěji predovaná, pokud byla umístěná při okraji rákosiny nebo porostu orobince navazujícím na sousední terestrický biotop (louku), zatímco hnízda umístěná uvnitř porostu a při jeho okraji sousedícím s vodní hladinou přežívala lépe. Velmi podobných výsledků dosáhli v pokusech s umělými hnízdy také Hansson *et al.* (2000). Z toho by bylo možné usuzovat, že rákosník velký si pro své hnízdění opravdu vybírá ty nejbezpečnější části rákosových a orobincových porostů. Bohužel další dvě studie s umělými hnízdy prokázaly trend buď spíše opačný (Báldi a Bátary 2005) nebo měnící se v čase (Bátary *et al.* 2004). A ani u reálných aktivních hnízd rákosníka velkého nebyla závislost mezi predací a jejich vzdáleností od okraje porostu prokázána (Hansson *et al.* 2000, Jelínek 2010).

Výsledky studií využívajících umělá hnízda a těch pracujících s reálnými aktivními hnízdy rákosníka velkého se výrazně lišily i v případě dalších prediktorů predace hnízd. Zatímco u umělých hnízd byla častěji predována časnější hnízda (Hansson *et al.* 2000, Trnka *et al.* 2009), ve studiích využívajících k analýzám robustních vzorků aktivních reálných hnízd žádný vliv načasování hnízdění prokázán nebyl (**Kapitola 2** – 817 hnízd, Bensch a Hasselquist 1994 – 279 hnízd, Hansson *et al.* 2000 – 121 hnízd). Podobně měly statisticky významný vliv na přežívání umělých hnízd i některé parametry hnízdního místa, jako kvalita rákosových stébel (jejich průměr) nebo hustota stébel v porostu kolem hnízda (Trnka *et al.* 2009), zatímco v případě reálných aktivních hnízd žádný takový vliv zaznamenán nebyl (Trnka *et al.* 2009, Hansson *et al.* 2000, Jelínek 2010). Nezdá se tedy, že by lepší ukrytí hnízda přinášelo jeho majitelům nějaké výhody v boji s predátory.

Nápadnost hnízda pro predátory by kromě parametrů okolního prostředí mohla ovlivňovat i jeho samotná velikost, a to obzvláště u druhu s tak značnou velikostní variabilitou hnízd, jakým je rákosník velký (obr. str. 66, **Kapitola 3, 4**). Výsledky prvních pokusů s umělými hnízdy takový vliv opět naznačovaly. López-Iborra *et al.* (2004) porovnávali přežívání neaktivních reálných hnízd rákosníka obecného a rákosníka velkého vnaděných křepelčími a modelínovými vejci a zjistili, že mnohem větší hnízda rákosníka velkého byla predována rychleji než menší hnízda rákosníka obecného. Tato studie ale bohužel trpí dvěma zásadními nedostatky, a to nedostatkem hnízd rákosníka velkého (25 hnízd rákosníka velkého vs. 230 hnízd rákosníka obecného), což zvyšuje vliv náhody na výsledky statistických analýz, a extrémně vysokou mírou predace experimentálních hnízd, jež zapříčinila i velmi nízkou variabilitu výsledků (predátoři vyplenili všechna experimentální hnízda rákosníka velkého a 96,5 % hnízd rákosníka obecného). Oba tyto nedostatky se podařilo odstranit v druhé experimentální studii zkoumající vliv velikosti hnízda rákosníka velkého na pravděpodobnost jeho predace (**Kapitola 3**). V ní bylo testováno přežívání dvojic neaktivních reálných hnízd rákosníka velkého vnaděných vejci zvonka zeleného (*Chloris chloris*) a konopky obecné (*Linaria cannabina*) plněnými modelínou. Každá dvojice (N = 50) se skládala z velkého a malého hnízda, kdy velké mělo dvojnásobnou velikost hnízda malého, umístěných v místech se stejnými parametry prostředí. Pravděpodobnost predace se ovšem mezi oběma velikostními typy hnízd nijak nelišila. Zdá se tedy, že velikost hnízda rákosníka velkého pravděpodobnost jeho vyplenění predátorem nijak nezvyšuje, což je i v souladu s poznatky získanými na reálných aktivních hnízdech rákosníka velkého (Moskát a Honza 2000) i jiných druhů ptáků (Lent 1992, Hatchwell *et al.* 1996, Palomino *et al.* 1998, Soler *et al.* 2001, Herranz *et al.* 2004, Suárez *et al.* 2005, Humphreys *et al.* 2007, ale ne Antonov 2004), případně v dalších experimentálních studiích využívajících různě velká hnízda stejného druhu (Creswell 1997, ale ne Møller 1990a) nebo dokonce různých druhů ptáků (Weidinger 2002, Weidinger 2004). Právě Weidinger (2002) ve své experimentální studii na vzorku

několika stovek hnízd ukázal, že na pravděpodobnost predace umělých hnízd neměla vliv jejich velikost (např. kos černý vs. pěnice černohlavá), ale pouze jejich umístění v prostředí.

Avšak ani sebepečlivější design nemůže odstranit hlavní nedostatek experimentů s umělými hnízdy. Jejich výsledky totiž mohou být zásadně ovlivněny tím, že některé druhy predátorů, plenících skutečná aktivní hnízda, se mohou těm umělým neaktivním například programově vyhýbat a naopak (Thompson *et al.* 2004). V **Kapitole 3** jsme se ovšem vypořádali i s tímto problémem, a to díky tomu, že se nám podařilo zvětšit i některá aktivní hnízda rákosníka velkého. Predaci těchto hnízd jsme pak porovnávali s podobným počtem náhodně vybraných kontrolních hnízd. Jednoznačný závěr tento experiment ovšem bohužel nepřinesl, neboť zvětšená hnízda byla predována častěji než hnízda kontrolní pouze marginálně nesignifikantně (P = 0,061). Podobně nebyl prokázán rozdíl mezi pravděpodobností predace zvětšených a zmenšených hnízd straky obecné (*Pica pica*, Soler *et al.* 2001).

Z výsledků všech výše zmíněných studií se tedy zdá, že velikost hnízda pravděpodobnost jeho vyplenění predátorem buď neovlivňuje vůbec, nebo je její vliv velmi malý a projeví se pouze u hnízd s opravdu extrémní velikostí (zvětšená hnízda z experimentu v **Kapitole 3**).

Velikost hnízda, stejně jako charakteristiky hnízdního místa a jeho okolí, sice jakýmsi relativně snadno měřitelným a pro vědce uchopitelných způsobem charakterizují jeho potenciální nápadnost pro predátory. Těžko nám ovšem prozradí, jak danou situaci vidí sami zkoumaní jedinci, tedy proč se jim to které hnízdní místo nebo celé teritorium vlastně tak líbí. Není proto nic jednoduššího, nebo v tomto případě spíše složitějšího, než posoudit kvalitu teritoria právě pomocí preferencí jedinců daného druhu. To se podařilo Benschovi a Hasselquistovi (1991) právě u rákosníka velkého, kdy ukázali, že atraktivita teritorií se dá nejlépe charakterizovat pomocí pořadí jejich obsazování přilétnuvšími samci. Ve své další studii (Hansson *et al.* 2000) pak ukázali, že takto měřená kvalita teritoria ovlivňuje i pravděpodobnost predace zde postavených hnízd, neboť hnízda v méně atraktivních teritoriích trpěla vyšší mírou predace než ta postavená v teritoriích atraktivnějších. To by se dalo vysvětlit přinejmenším dvěma způsoby. V atraktivnějších teritoriích by měly hnízdit kvalitnější páry, které budou svá hnízda lépe bránit. Zároveň by atraktivnější teritoria mohla být opravdu bezpečnější. Pro druhou možnost svědčí to, že v atraktivnějších teritoriích měla nižší pravděpodobnost predace nejen reálná aktivní hnízda, ale i hnízda experimentální.

Kvalitu teritoria, nebo v tomto případě spíše hnízdního místa, nám kromě jeho majitelů může nepřímo poodhalit i další druh, který má k hnízdům rákosníků velmi blízký vztah – kukačka obecná. Jak již bylo řečeno v kapitole zabývající se hnízdním parazitizmem, kukačka si k parazitaci vybírá spíše hnízda hůře ukrytá, která se jí v prostředí lépe hledají (**Kapitola 1**, Øien *et al.* 1996, Moskát a Honza 2000, Clarke *et al.* 2001). Parazitovaná hnízda by proto měla být i častěji predována, což se ve fázi inkubace podařilo prokázat v **Kapitole 2** jak u rákosníka velkého, tak i u příbuzného rákosníka obecného. Rozdíl mezi neparazitovanými a parazitovanými hnízdy ovšem ve fázi mláďat téměř vymizel. Mláďata obou těchto hostitelských druhů nebyla na hnízdech predována častěji než stejně stará mláďata kukaček (do devátého dne věku). Pokud byla ale porovnávána predace hnízd obsahujících mláďata rákosníků (do devátého dne věku) a hnízd se staršími kukačkami (od devátého do sedmnáctého dne věku) ukázalo se, že starší kukačky jsou na hnízdech predovány častěji u rákosníka obecného, ale ne u rákosníka velkého. To naznačuje, že kukačky by mohly být penalizovány za svoje intenzivní a hlasité žadonění (Kilner and Davies 1999, Butchart *et al.* 2003) přinejmenším u některých druhů hostitelů, například u málo agresivního rákosníka obecného (Čapek *et al.* 2010).

O pravděpodobnosti predace hnízd rákosníka velkého a faktorech, které ji ovlivňují, toho tedy bylo ve světové vědecké literatuře napsáno poměrně hodně. Drobným nedostatkem v poznání ovšem zůstává to, že vlastně vůbec nevíme, kdo je za tuto predaci hnízd odpovědný. Doposud totiž téměř všichni výzkumníci využívali k identifikaci predátorů hnízd rákosinových druhů pěvců pouze vlastní fantazii v kombinaci se stopami, které predátoři zanechali na modelínových vejcích v umělých hnízdech (např. **Kapitola 3**, Bensch a Hasselquist 1994, Hansson *et al.* 2000), což je ovšem v dnešní době, kdy

se již rutinně používají miniaturní kamerové sety nahrávající veškeré dění přímo na hnízdě, naprosto nedostatečné (Thompson *et al.* 2004, DeGregorio *et al.* 2014). Existují tak pouze dvě přímá pozorování ze Švédska z jezera Kvismaren, kde Bensch a Hasselquist (1994) pozorovali predaci hnízda rákosníka velkého lyskou černou (*Fulica atra*) a norkem americkým (*Mustela vison*) a jedno z Mutěnických rybníků, kde byla nafilmována predace hnízda rákosníka velkého samicí kukačky. Ta již během inkubace odnesla dvě ze tří vajec v hnízdě, které bylo následně opuštěno (Jelínek a Šulc nepublikované údaje). U hnízd ostatních rákosinových druhů je situace obdobná. Pouze u rákosníka obecného existuje v současné době pět videonahrávek predací jeho hnízd obsahujících starší mládě kukačky (Jelínek a Šulc nepublikované údaje). Ve dvou případech byla predátorem kuna (*Martes sp.*, viz obr. str. 43), v jednom lasice kolčava (*Mustela nivalis*). Ve dvou zbývajících případech se z nahrávky identita predátora nedala určit, ale pravděpodobně se také jednalo o lasicovitou šelmu, případně kočku. Vzhledem k tomu, že se jedná v zásadě o anekdotická pozorování, by bylo v budoucnu velmi vhodné věnovat identifikaci predátorů rákosinových druhů pěvců mnohem větší úsilí, a to i kvůli interpretaci či evaluaci výsledků starších predačních studií s umělými hnízdy (např. Hansson *et al.* 2000).

Hnízdo jako signál

Ptačí hnízdo většinou plní funkce ryze praktické – vytváří prostor, kam samice snáší vejce, poskytuje jim oporu, izoluje snůšku od vnějšího prostředí apod. Je ovšem poměrně dobře známo, že u některých druhů slouží i jako sekundární pohlavní znak (Hansell 2000). Klasickými příklady takových druhů jsou snovači (Ploceidae, Collias a Victoria 1978, Lawes *et al.* 2002), střízlíci (Troglogytidae, Evans a Burn 1996), nebo moudivláček lužní (*Remiz pendulinus*, Persson a Öhrström 1989), u nichž si samice podle kvality hnízda vybírají své partnery. Samice těchto druhů většinou provádí inspekce nově postavených hnízd, a když se jim některé z nich zalíbí, vyberou si ho pro hnízdění (Persson a Öhrström 1989, Evans a Burn 1996). Poté, co se takto pro některého ze samců rozhodnou, stává se z jeho hnízda opět „pouze" praktická součást reprodukce.

U většiny ostatních ptačích druhů ovšem není stavba hnízda výhradně v gesci samce, ale podílí se na ní buď v zásadě rovnocenně oba partneři, nebo ho celé staví samice (Hansell 2000). Hnízdo je zároveň stavěno až poté, co dojde k vytvoření páru a jeho kvalita tedy v pohlavním výběru nijak nevystupuje. Ale i v tomto případě by hnízdo jako určitý dorozumívací prostředek mezi partnery sloužit mohlo. Tato hypotéza postkopulačního signálu kvality („sexual display hypothesis", Moreno *et al.* 1994, Soler *et al.* 1998b) vychází z principu rozdílného rozložení rodičovských investic během rozmnožování („differential allocation hypothesis", Burley 1986, Sheldon 2000). Ten předpokládá, že investice do rozmnožování bude úměrná kvalitě partnera. Pokud se tedy danému jedinci podaří spárovat s nadprůměrně kvalitním partnerem, měl by do rozmnožování investovat více, neboť jeho potomci budou také kvalitnější. Pokud se ovšem danému jedinci podaří spárovat pouze s podprůměrně kvalitním partnerem, měl by do současné reprodukce investovat naopak méně a raději šetřit energii do dalších reprodukčních cyklů. Jestliže se méně kvalitní partneři nechtějí s nízkým reprodukčním úspěchem spokojit, mohou menší úsilí svých kvalitnějších partnerů buď kompenzovat svojí zvýšenou aktivitou, nebo je svou zvýšenou aktivitou dokonce stimulovat k většímu zapojení do reprodukce (Soler *et al.* 1998b). K tomu ovšem potřebují určité komunikační nástroje, aby tuto svou zvýšenou ochotu zapojit se do reprodukce svým partnerům mohli signalizovat. A právě hnízdo, respektive jeho velikost, odrážející úsilí, které jedinec investoval do jeho stavby, by mohlo sloužit jako takový signál.

Prvním předpokladem platnosti hypotézy postkopulačního signálu kvality by tedy mělo být to, že páry s většími hnízdy budou i více investovat do rozmnožování, což se podařilo prokázat u několika ptačích druhů, u nichž byla zjištěna korelace mezi velikostí hnízda a různými reprodukčními charakteristikami. Samice vlaštovek obecných (*Hirundo rustica*, Møller 1982), pěvců ryšavých (*Cercotrichas*

galactotes, Palomino *et al.* 1998) a rákosníků velkých (**Kapitola 4**) snášely do větších hnízd více vajec. Tučňáci uzdičkoví (*Pygoscelis antarctica*) a rákosníci velcí hnízdící ve větších hnízdech měli i větší hnízdní úspěšnost (**Kapitola 4**, Moreno *et al.* 1995). Rákosníci velcí a samci pěvce ryšavého hnízdící ve větších hnízdech krmili svá mláďata s větším úsilím (Palomino *et al.* 1998, Avilés *et al.* 2009) a tato mláďata měla i větší hmotnost a častěji se vracela v následujících letech do rodné oblasti (**Kapitola 4**).

Žádný z těchto příkladů ovšem nedokazuje, že hnízdo slouží jako signál v komunikaci mezi partnery. Veškeré výše zmíněné výsledky jsou totiž založeny na vzájemných korelacích a velikost hnízda tak může odrážet pouze dobrou kondici jeho stavitelů (Soler *et al.* 1998a, Mainwaring a Hartley 2009), kteří si díky tomu mohou snadno dovolit lehké navýšení investice do stavby hnízda (Lambrechts *et al.* 2012) například proto, aby zlepšili jeho odolnost vůči vlivům vnějšího prostředí (Fargallo *et al.* 2001). Zároveň je sice možné, že aktivita jedince při stavbě hnízda může odrážet jeho ochotu investovat do následné reprodukce, jako je tomu u samců vlaštovek obecných (Soler *et al.* 1998a), a přesto stavební aktivita jako signál sloužit nemusí. Partneři, v tomto případě samice, se totiž mohou orientovat podle jiných znaků, například délky ocasních per, která u vlaštovek odráží jak kvalitu a atraktivitu samce (Møller 1990b), tak i jeho ochotu podílet se na reprodukci (Møller 1994).

Pokud ale hnízdo jako signál skutečně slouží, měla by jeho velikost daleko spíše korelovat s kvalitou nikoliv stavitele (toho, kdo signalizuje), ale jedince, který hnízdo nestaví (toho, kdo signál přijímá). Taková korelace byla prokázána u sýkory koňadry (*Parus major*), druhu, u něhož staví hnízdo výhradně samice (Cramp 1992). Velikost hnízda totiž pozitivně korelovala se sytostí zbarvení samčího opeření (Broggi a Senar 2009), což by nasvědčovalo tomu, že samice chtěly kvalitnějším samcům (Horak *et al.* 2001, Senar *et al.* 2008) signalizovat svoji větší ochotu investovat do reprodukce.

Abychom mohli odlišit, zda je velikost hnízda signálem kvality jedince, nebo pouze jejím korelátem, musíme ovšem provést experiment a s velikostí hnízda manipulovat. První takový experiment provedli Soler *et al.* (2001) u straky obecné (*Pica pica*), u níž staví hnízdo z větší části samec (Cramp 1992) a kde velikost hnízda koreluje s jeho stavebním úsilím a kvalitou (Soler *et al.* 1998a). Strači hnízda si v tomto experimentu rozdělili do skupin a manipulovali s velikostí jejich střech. Samice strak, jimž bylo hnízdo zmenšeno, snášely menší snůšky a jejich mláďata se líhla výrazně asynchronněji než ta, kterým bylo hnízdo zvětšeno, případně ta, jimž s velikostí střechy hnízda manipulováno nebylo (Soler *et al.* 2001). Další tři experimenty pak byly provedeny u druhů, u kterých staví hnízda pouze samice, a změna velikosti hnízda by proto měla ovlivnit samčí investici do reprodukce. Ve studiích Tomáse *et al.* (2013) u sýkory modřinky (*Cyanistes caeruleus*) a Cantarera *et al.* (2016) u brhlíka lesního (*Sitta europaea*) autoři prokázali, že samci obou druhů reagovali na manipulaci s velikostí hnízda změnou tzv. „risk taking indexu" vyjádřeného v tomto případě ochotou jedince vrátit se do hnízda poté, co bylo kontrolováno výzkumníky. Výsledky obou studií se ale trochu lišily v detailech. Zatímco samci sýkor modřinek, kterým bylo hnízdo zmenšeno, byli plašší než samci ze zvětšených a kontrolních nemanipulovaných hnízd, samci brhlíků, jimž byla hnízda zvětšena, byli odvážnější a rychleji přilétali zkontrolovat hnízdo po disturbanci než samci z kontrolních hnízd, častěji také při této kontrole předběhli samice. Obě studie ovšem nezaznamenaly, že by samci na změnu velikosti hnízda reagovali zvýšením případně snížením svého úsilí během krmení mláďat vyjádřeného pomocí frekvence příletů s potravou.

Frekvence příletů s potravou („feeding rate") je snadno a zároveň přesně měřitelná reprodukční charakteristika, která je běžně využívaná ve vědeckých studiích. Bohužel její velkou nevýhodou je, že vůbec nemusí odrážet množství potravy, které daný jedinec mláďatům ve skutečnosti přinese. Například Palomino *et al.* (1998) ukázali, že i v případě stejných frekvencí příletů s potravou se mohou krmící ptáci významně lišit ve velikostech jednotlivých soust, která mláďatům přinášejí. Ve skutečnosti se tak celkové množství potravy, které mláďatům nanosí, mezi jedinci významně liší, ačkoliv frekvence jejich příletů s potravou může být srovnatelná. Je proto možné, že i ve studiích Tomáse *et al.* (2013) a Cantarera *et al.* (2016) nebyla zaznamenána závislost mezi samčí investicí do krmení mláďat a experi-

mentální manipulací s velikostí hnízd právě z tohoto důvodu. V poslední experimentální studii zabývající se rolí velikosti hnízda v signalizaci mezi partnery jsme proto použili místo frekvencí příletů s potravou právě její celkové množství, které rodiče mláďatům přinesli (**Kapitola 4**). V této studii byla zvětšována hnízda rákosníků velkých prakticky na jejich dvojnásobek (a to zhruba na maximum přirozeně se vyskytující variability), část hnízd pak byla ponechána jako kontroly. Samci, jejichž hnízda byla zvětšena, pak skutečně na tuto manipulaci reagovali a přinášeli mláďatům i více potravy, zatímco množství potravy přinášené samicemi se mezi experimentálními skupinami nelišilo. Zároveň se ovšem nepodařilo prokázat, že by množství potravy, které samec přinese mláďatům, korelovalo s velikostí hnízda u druhé nemanipulované skupiny hnízd. Tato hnízda byla ovšem celkově mnohem menší, než hnízda po experimentálním zvětšení (**Kapitola 4**). Je proto možné, že reakci samců může vyvolat pouze značně nadprůměrná velikost hnízda, případně se samci mohou řídit ještě podle dalších signálů, které samice mohou v komunikaci s nimi používat.

Z množství výše popsaných studií je zřejmé, že roli hnízda jako signálu komunikace mezi partnery byla věnována relativně značná pozornost výzkumníků. Poměrně robustní korelační evidenci v současné době doplnilo několik důležitých experimentů manipulujících s velikostí hnízda. Výsledky těchto pokusů bohužel rozhodně nejsou jednoznačné, neboť i když jedinci na experimentální změnu velikosti hnízda reagovali změnou některých parametrů reprodukčního úsilí, jiné velmi důležité parametry manipulace nijak neovlivnila. Pokud ovšem velikost hnízda jako komunikační signál mezi partery slouží, měli by tomu příjemci tohoto signálu přizpůsobit celé své reprodukční úsilí a nikoliv jen jednu jeho část, například obranu hnízda, nebo úsilí během krmení mláďat. Bylo by proto vhodné, aby se roli hnízda v signalizaci věnovalo i nadále alespoň tolik pozornosti, co v současné době.

Hnízdní kotlinka a její optimalizace

Typické ptačí hnízdo se skládá ze čtyř základních částí (Hansell 2000). Strukturní vrstva tvoří hlavní část – hmotu hnízda, připojovací elementy připevňují hnízdo k podkladu a vnější (dekorativní) vrstva pak dotváří jeho vzhled, maskuje ho před predátory (Hansell 1996), případně ještě vylepšuje jeho fyzikální vlastnosti (Hilton *et al.* 2004). Čtvrtou částí je pak výstelka hnízdní kotlinky. Ta je většinou tvořena značně odlišnými materiály než zbývající části hnízda, neboť se jako jediná dostává do přímého kontaktu s vejci (McGowan 2004, Pinowski *et al.* 2006) a zároveň tepelně izoluje obsah hnízda od venkovního prostředí (Franklin 1995, Mainwaring *et al.* 2012). Například u rákosníka velkého je výstelka hnízdní kotlinky tvořena prakticky výlučně rákosovými latami, které jsou velmi jemné a nejsou využívány pro stavbu ostatních částí hnízda (Kožená-Toušková 1973, vlastní pozorování).

Na vlastnostech výstelky a hnízdní kotlinky jako celku tedy závisí i účinnost inkubace (Reid *et al.* 2002, Heenan 2013). Mělčí hnízda a hnízda s méně kompaktními stěnami chrání svůj obsah před větrem hůře, což způsobuje rychlejší vychládání vajec, a zvyšuje tak energetické náklady na inkubaci (Skowron a Kern 1980, Kern 1984, Heenan a Seymour 2012). Kompaktnost stěn, i když je pro izolační vlastnosti hnízda zásadní (Kern 1984), se ovšem velmi komplikovaně měří. Proto se mnohem častěji pro charakteristiku izolačních schopností hnízda používá tloušťka jeho stěny. Ta může být navíc relativně dobrou charakteristikou tepelných vlastností hnízda, obzvlášť pokud se hnízda mezi sebou příliš neliší právě v kompaktnosti svých stěn (Whittow a Berger 1976, Skowron a Kern 1980). Že tomu tak u mnoha druhů může být, nepřímo potvrzují studie ukazující, že ptáci hnízdící v chladnějších oblastech (větších zeměpisných šířkách a vyšších nadmořských výškách) staví hnízda s tlustšími stěnami (Collias a Collias 1971, Mainwaring *et al.* 2014), případně silnější výstelkou (Mainwaring *et al.* 2012), podobně jako jedinci hnízdící dříve v hnízdní sezoně (Franklin 1995, Herranz *et al.* 2004, Suárez *et al.* 2005). Mainwaring *et al.* (2014) zároveň ukázali, že ačkoliv hnízda se zvětšující se zeměpisnou šířkou zvětšovala svou vlastní šířku, tento nárůst byl způsoben pouze změnou v tloušťce stěny a nikoliv změnou

velikosti hnízdní kotlinky. Její šířka se totiž se zeměpisnou šířkou nijak neměnila. To ukazuje, že velikost hnízdní kotlinky může být ovlivňována i jinými selekčními tlaky než tlakem na co nejnižší energetické náklady na inkubaci.

Velikost hnízdní kotlinky by totiž měla být uzpůsobena také tomu, aby bezproblémově pojmula svůj obsah, ať už to jsou vejce, nebo později mláďata („hypotéza ideální velikosti snůšky" - Snow 1978). Počet vajec ve snůšce se totiž i v rámci jednoho ptačího druhu může poměrně značně lišit. Například u rákosníka velkého to v drtivé většině případů bývá mezi třemi a šesti vejci (vlastní nepublikované údaje). Rozměry kotlinky by proto měly odpovídat jak počtu vajec, která do ní budou snesena, tak především počtu mláďat, která se z těchto vajec vylíhnou. Příliš velká kotlinka by mohla zhoršovat efektivitu inkubace, zatímco příliš malá by nemusela být schopná pojmout rychle rostoucí mláďata (Slagsvold 1982), i přesto, že se její šířka pod jejich náporem v průběhu hnízdění zvětšuje (Slagsvold 1989). Druhý z těchto předpokladů experimentálně potvrdil Slagsvold (1982), který zvětšil počet vajec a následně tedy i mláďat v hnízdech drozda kvíčaly (*Turdus pilaris*) z pěti na šest, nebo sedm. Pokud byla všechna mláďata stejně stará, nemělo zvětšení jejich počtu v hnízdě žádný vliv na jejich úspěšné vyvedení. Pokud ale mláďata stejně stará nebyla, byla ta nejmladší často nacházena vypadlá pod hnízdem, neboť pravděpodobně nebyla schopná obstát v boji o místo se svými staršími a většími sourozenci. Slagsvold (1982) také ukázal, že kvíčaly, jimž vyměnil jejich hnízda za větší, vyváděly zvětšené snůšky mnohem lépe než ty s kontrolními nezměněnými hnízdy. Stejný výsledek měly i podobné pokusy s pěnkavou obecnou, a dokonce i s dutinovými druhy lejskem černohlavým (*Ficedula hypoleuca*)a sýkorou koňadrou (Slagsvold 1989).

Výsledky těchto pokusů ale mohou odrážet pouze logický fakt, že musí existovat určitá velikost hnízdní kotlinky, kdy už se do ní mláďata fyzicky zkrátka nemohou vejít, případně je kotlinka již tak velká, že se inkubace vajec stane velmi neefektivní. To ovšem hnízdící samice nemusí vůbec vnímat, neboť je možné, že za normálních okolností vždy postaví tak velkou kotlinku, jež její snůšku a z ní vylíhlá mláďata bezproblémově pojme. Proto pokud hypotéza ideální velikosti snůšky platí, musí velikost hnízdní kotlinky korelovat s počtem vajec ve snůšce i u přirozených nijak nemanipulovaných hnízd. Tento předpoklad byl potvrzen u lindušky úhorní (*Anthus campestris*, Suárez *et al.* 2005 – objem kotlinky), pěvce ryšavého (Palomino *et al.* 1998 – objem kotlinky) a rákosníka velkého (**Kapitola 5** – hloubka, ale ne šířka kotlinky), zatímco u skřivánka krátkoprstého (*Calandrella brachydactyla*) a skřivana polního (*Alauda arvensis*, Herranz *et al.* 2004 – šířka a hloubka kotlinky) potvrzen nebyl.

Aby hnízdní kotlinka dostala svůj výsledný miskovitý tvar, používají ptáci při její stavbě své tělo, kdy hrudí tlačí na stěny kotlinky a tvarují je tak do konečné podoby (např. Kluyver 1955, **Kapitola 5**). Díky tomu by větší ptáci měli stavět i větší hnízda a zároveň by mohli snášet i více vajec, protože jsou také, díky své velikosti, kvalitnější (Labocha a Hayes 2012). To se podařilo prokázat v **Kapitole 5**, kdy bylo zjištěno, že větší samice rákosníka velkého stavějí opravdu i širší a hlubší hnízdní kotlinky během svých prvních hnízdění v sezoně. To by naznačovalo, že by stavící jedinci velikost kotlinky přímo ovlivňovat nemuseli a snížená hnízdní úspěšnost v důsledku její nevhodné velikosti by byla pouze nutným a nevyhnutelným zlem, které se může projevit jen v relativně méně častých situacích, například pokud v hnízdě nejsou stejně stará mláďata (Slagsvold 1982).

Pokud jsou tedy hlavní příčinou pozitivní korelace mezi velikostí snůšky a rozměry kotlinky mechanické zákonitosti její stavby, měli by stejní jedinci stavět v různých hnízdech stejně velké kotlinky. V jediné studii, ve které byl tento předpoklad testován (**Kapitola 5**), jsme ovšem došli k opačnému závěru, neboť náhradní hnízda stavěná týmiž samicemi rákosníka velkého měla významně užší a mělčí kotlinky než kotlinky prvních hnízd postavených ve stejné hnízdní sezoně. Je tedy zřejmé, že ačkoliv velikost kotlinky rákosníka velkého je ovlivněna velikostí samice, která ji postavila, není to jediný faktor, který ji ovlivňuje. Dalšími faktory mohou být právě snaha o přizpůsobení rozměrů kotlinky velikosti snůšky, případně snaha o co nejlepší izolační vlastnosti hnízda. Druhý z těchto faktorů ovšem pro vy-

světlení rozdílu ve velikosti kotlinky mezi prvními a náhradními hnízdy rákosníka velkého nestačí, neboť se oba typy hnízd mezi sebou v šířce stěny neliší (**Kapitola 5**), ačkoliv jsou náhradní hnízda z definice stavěna později než hnízda první. Snaha o přizpůsobení velikosti kotlinky počtu vajec ve snůšce se tedy jeví jako nejpravděpodobnější faktor, který velikost kotlinky spolu s rozměry samice ovlivňuje. Bohužel jednoduché porovnání prvních a náhradních hnízd do tohoto problému více světla opět nevneslo, neboť se spolu s hnízdní kotlinkou zmenšovala i samotná hnízda (**Kapitola 5**), a velikost kotlinky se tak s velikostí celého hnízda mohla pouze druhotně „svézt". Proto byl proveden ještě dodatečný test, v němž byly porovnávány změny v hloubce a šířce kotlinky dvojic prvních a náhradních hnízd postavených stejnou samicí se stejnou velikostí snůšky (např. obě po pěti vejcích) a obdobných dvojic prvních a náhradních hnízd téže samice s rozdílnou velikostí snůšky (např. první hnízdo pět vajec a náhradní čtyři vejce). Ten ukázal, že rozdíl v šířce kotlinky byl u dvojic hnízd, kde měla náhradní hnízda o jedno vejce menší snůšku než hnízda první, větší než u dvojic prvních a náhradních hnízd, kde se počet vajec ve snůšce nezměnil. Tento rozdíl byl ale bohužel pravděpodobně kvůli malé velikosti vzorku (9 vs. 14 hnízd) pouze marginálně nesignifikantní (**Kapitola 5**).

Z výsledků výše zmíněných studií se tedy zdá, že velikost kotlinky bude ovlivňována více faktory a snaha samic přizpůsobit její rozměry počtu vajec, které do ní hodlají snést, bude jen jedním z nich. Navíc důkazy, které by tuto možnost podporovaly, zatím stále nejsou úplně přesvědčivé a studií, jež by porovnávaly velikost kotlinky u hnízd postavených stejnými jedinci, je velký nedostatek. Studie, která využila přírodní experiment a porovnávala hnízda postavená stejnými jedinci v různých letech s různě velkými snůškami, pak chybí úplně. Zároveň ovšem není možné vyloučit ani teoretickou možnost, že by naopak samice přizpůsobovaly počet snesených vajec velikosti kotlinky, jak ukazují studie Löhrla (1973, 1980) provedené na sýkoře koňadře. Ty totiž reagovaly na změnu vnitřní velikosti budky v průběhu hnízdění změnou velikosti snůšky v předpokládaném směru. Pokud se jim budka zvětšila, snesly i více vajec a naopak. Výsledky těchto studií ovšem není možné automaticky přenášet i na další druhy ptáků a obzvlášť ne na druhy stavějící otevřená miskovitá hnízda. Dá se totiž předpokládat, že na sýkory koňadry, stejně jako na další druhy ptáků, hnízdící v sekundárních dutinách, bude selekce na optimální velikost snůšky působit velmi silně. Dutin vhodných ke hnízdění je totiž v přirozeném prostředí spíše nedostatek (Camprodon *et al.* 2008) a zároveň se velikostně navzájem velmi liší (Wesołowski 2003). Schopnost sýkor přizpůsobit snůšku velikosti dutiny se proto dá očekávat mnohem spíše než u otevřeně hnízdících druhů pěvců, kteří nejsou při stavbě hnízda v zásadě nijak prostorově omezeni.

Závěr

A proč tedy někteří rákosníci velcí staví dvakrát větší hnízda než jiní? Upřímná a pravdivá odpověď zní, že stále nevíme. Ne že by naše znalosti byly na stejné úrovni jako před deseti lety, tak tomu rozhodně není. Je třeba ovšem konstatovat, že, ač se to může zdát jako klišé, pro komplexní zhodnocení faktorů, které by udržovaly velikostní polymorfismus rákosničích hnízd, stále nemáme dostatek informací. A to i přes značné úsilí, které jsme výzkumu této problematiky věnovali. Buď se nám z časových či jiných důvodů některé hypotézy nepodařilo otestovat vůbec, nebo se je sice otestovat povedlo, ale příroda s námi ne vždy byla ochotna spolupracovat natolik, aby byly výsledky těchto našich studií dostatečně jednoznačné. Spíše se nám proto podařilo zjistit, co za velikostní variabilitu rákosničích hnízd nemůže, než co k jejímu udržení přispívá.

Například je celkem jisté, že velikost hnízda rákosníka velkého nijak neovlivňuje to, zda bude parazitováno kukačkou (**Kapitola 1**) a asi jen velmi málo to, zda bude vypleněno predátorem (**Kapitola 3**). Velikost hnízda by ovšem mohla fungovat jako signál kvality samice, neboť se zdá, že samci rákosníků velkých krmí mláďata z větších hnízd více (**Kapitola 4**). Pokud by tomu tak ovšem bylo, musela by být podle teorie signalizace stavba velkého hnízda pro samice nákladná (Maynard-Smith a Harper 2003), ať již samotnými energetickými nároky na jeho stavbu, o jejichž velikosti nemáme dosud ani

matnou představu, nebo právě vlivem tlaku predátorů. Ten se ovšem nezdá být příliš silný, neboť hnízda rákosníka velkého patří k nejméně predovaným hnízdům pěvců vůbec (**Kapitola 2**). A pokud má velikost hnízda na pravděpodobnost jeho predace vůbec nějaký vliv, pak spíše zanedbatelný, který se projeví jen u malého počtu extrémně velkých hnízd (**Kapitola 3**). Zda je velikost hnízda, v tomto případě především šířka, ovlivněna snahou samice postavit takovou kotlinku, jež bude svou velikostí odpovídat počtu vajec, která do ní snese, a především počtu mláďat, která se z těchto vajec vylíhnou, také není úplně jisté, ačkoliv naše výsledky naznačují, že by tomu tak být opravdu mohlo (**Kapitola 5**). Šířka hnízda by mohla být ovlivněna i tlakem na jeho optimální termoregulační vlastnosti. Jaké tyto vlastnosti u různě velkých hnízd jsou, se nám ovšem stanovit, především z časových důvodů, nepodařilo.

Stále proto připadá v úvahu i možnost, že je velikost hnízda rákosníků velkých ovlivněna i jinými než adaptivními mechanismy. Méně šikovným samicím by například mohlo jít mnohem hůře uchytit stavební materiál mezi rákosová stébla, a základ strukturní části hnízda a následně i celé hnízdo by kvůli tomu byly mnohem větší než hnízda starších zkušenějších samic. Zároveň by velikost hnízda mohla být i důsledkem vrozených i naučených stavebních schopností a dovedností dané samice. Stejné samice by tudíž mohly stavět podobně velká i vypadající hnízda po celou hnízdní sezonu, případně po celý život. Vlivu věku, zkušeností samice ani vnitrosezónní případně meziroční tvarové a velikostní variabilitě hnízd stejných samic jsme se ale zatím bohužel téměř nevěnovali.

Je tedy zřejmé, že mnoho otázek týkajících se významu velikosti hnízda u rákosníka velkého, či u ptáků vůbec ještě stále čeká na své zodpovězení. Přesto jsem přesvědčen, že se mi během mého doktorského studia alespoň na několik otázek týkajících se významu velikosti hnízda u rákosníka velkého odpovědět podařilo.

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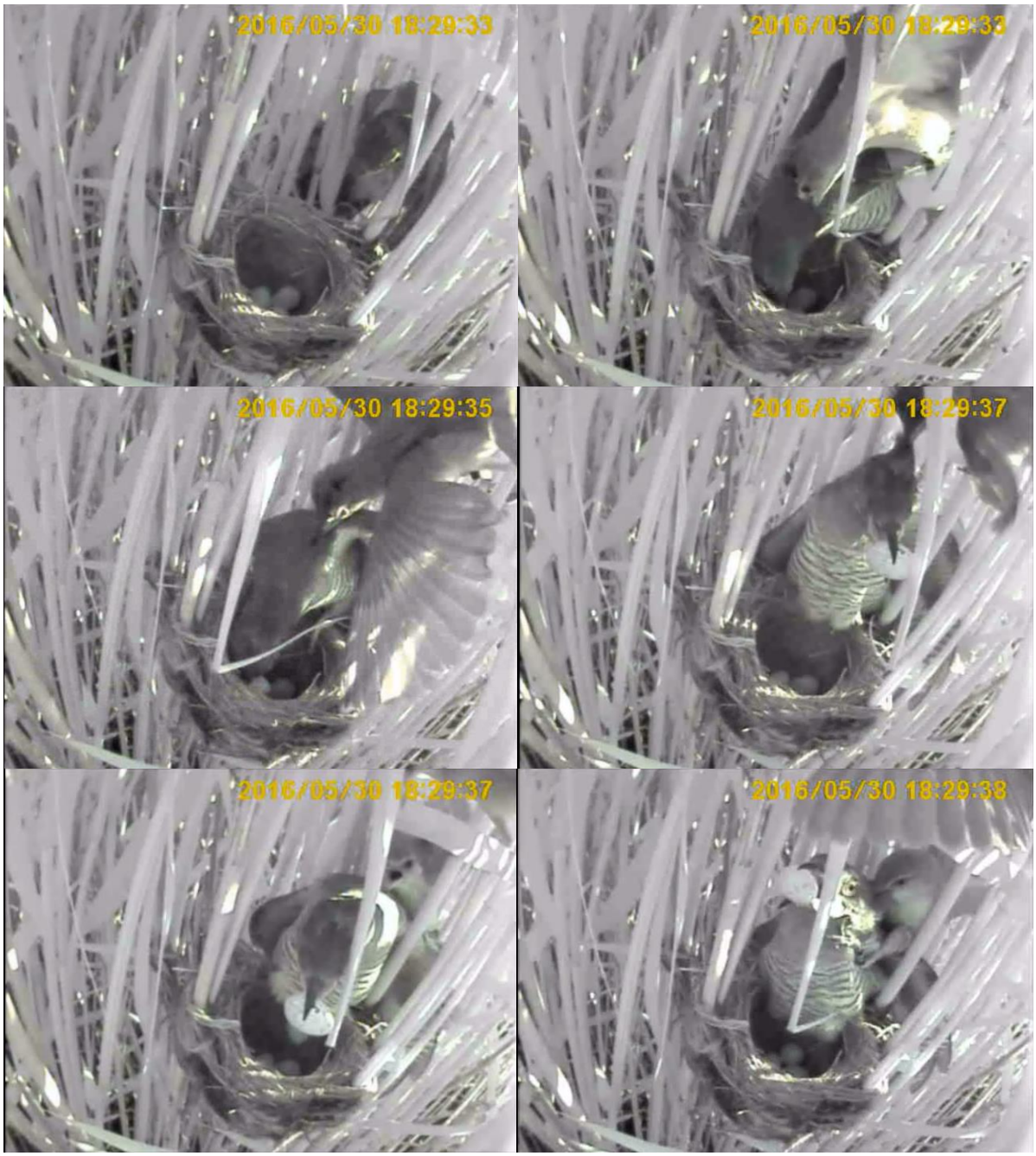
Přiložené rukopisy

Kapitola 1

Jelínek V., Procházka P., Požgayová M. & Honza M. (2014) Common cuckoos *Cuculus canorus* change their nest-searching strategy according to the number of available host nests. *Ibis* 156: 189-197.



Záznam průběhu parazitace hnízda rákosníka velkého (*Acrocephalus arundinaceus*) kukačkou obecnou (*Cuculus canorus*).

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Common Cuckoos *Cuculus canorus* change their nest-searching strategy according to the number of available host nests

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In recent decades, numerous studies have examined factors affecting risk of host nest parasitism in well-known avian host–parasite systems; however, little attention has been paid to the role of host nest availability. In accordance with other studies, we found that nest visibility, reed density and timing of breeding predicted brood parasitism of Great Reed Warblers *Acrocephalus arundinaceus* by the Common Cuckoo *Cuculus canorus*. More interestingly, hosts had a greater chance of escaping brood parasitism if nesting was synchronized. Cuckoo nest searching was governed primarily by nest visibility at high host-nest density. However, even well-concealed nests were likely to be parasitized during periods when just a few hosts were laying eggs, suggesting that Cuckoos adjust their nest-searching strategy in relation to the availability of host nests. Our results demonstrate that host vulnerability to brood parasitism varies temporally and that Cuckoo females are able to optimize their nest-searching strategy. Moreover, our study indicated that Cuckoos always manage to find at least some nests to parasitize. Thus, in this case, the co-evolutionary arms race should take place mainly in the form of parasitic egg rejection rather than via frontline pre-parasitism defence.

Keywords: brood parasitism, cuckoo perch, edge effect host aggression, host choice, nest height, nest visibility, nest volume.

Brood parasitism can result in a considerable decrease in the breeding success of host populations (Ortega & Ortega 2003, Barabás *et al.* 2004, Jewell & Arcese 2008, but see Brooker & Brooker 1996), or at least of individual hosts (Davies 2000). The impact of brood parasitism on host fitness, however, differs significantly between host–parasite systems. The most detrimental effect occurs in hosts of evicting cuckoos (Cuculidae) or honeyguides (Indicatoridae) where brood parasitism has an even greater impact than nest predation, since predation at least allows immediate re-nesting. Successful brood parasitism, on the other hand, precludes re-nesting and confers lower, or even no host breeding success (Payne & Payne 1998, Davies 2000). Thus, hosts have evolved numerous strategies to defeat their parasitic enemies. Two lines of defence can be distinguished: (1) defence preventing brood parasitism; and (2) defence after brood parasitism has occurred, such as nest desertion or egg ejection. The first includes nest guarding, aggressive host behaviour against adult parasites, breeding at sites safe from brood parasites or inconspicuous behaviour near the nest (Robertson & Norman 1977, Patten *et al.* 2011, Feeney *et al.* 2012).

Several hypotheses have been put forward to explain nest-site safety in terms of brood parasitism, including distance to the nearest perch site (Alvarez 1993, Hauber & Russo 2000), nest concealment or cover (Burhans 1997, Clarke *et al.* 2001), nest height above the ground (Clotfelter 1998, Banks & Martin 2001) and distance to habitat edge (Moskát

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& Honza 2000, Patten *et al.* 2006) or other active host nests (Spautz 1999). Other hypotheses emphasize host behaviour, such as physical (Sharp & Kus 2006) or acoustic (Gochfeld 1979) activity near the nest and aggression towards a brood parasite. The role of host aggression is equivocal as it may serve both as a nest-searching cue for brood parasites – 'nesting cue hypothesis' (Fiorini *et al.* 2009) – or as a means of driving them off – 'nest defence hypothesis' (Robertson & Norman 1977). In addition, the timing of breeding (Patten *et al.* 2011), nest size (McLaren & Sealy 2003) or height of the nearest perch site (Antonov *et al.* 2006) have been shown to affect the probability of parasitism. All these factors can be influenced by individual hosts, i.e. hosts can build nests far from trees, in denser vegetation or can be more aggressive in order to expel brood parasites. There are other factors, however, that hosts cannot influence or, at best, influence very little. For example, it is reasonable to expect that the probability of brood parasitism increases with increasing numbers of brood parasites present in the locality, or with decreasing numbers of breeding host pairs. Brood parasites lay a finite number of eggs per season and make use of a limited time-window successfully to parasitize individual host nests (Davies 2000). These constraints should favour host pairs breeding simultaneously, providing them with a better chance of avoiding parasitism through, for example, better nest concealment.

This scenario would represent an important density-dependent mechanism with a substantial role in brood parasitism, influencing the probability of parasitism at the population level much more than nest-site characteristics, for example. To our knowledge, however, only two studies have tested this hypothesis directly. Martínez *et al.* (1996) found that Eurasian Magpie *Pica pica* pairs that nested synchronously were parasitized by the Great Spotted Cuckoo *Clamator glandarius* less than non-synchronous pairs, and Clark and Robertson (1979) observed a similar relationship in Mangrove Warblers *Setophaga petechia* parasitized by Brown-headed Cowbirds *Molothrus ater*. It is quite surprising that there has been no evidence provided to date that such a density-dependent mechanism influences the likelihood of parasitism in hosts of the Common Cuckoo *Cuculus canorus* (hereafter Cuckoo), despite female Cuckoos parasitism being host-specific and the probable impact of the relationship being likely to be more important than in cowbird hosts.

Of importance in this context is that the numbers of brood parasites and hosts fluctuates between years, and hence the proposed density-dependent relationship could be influenced by their phenology. Cuckoos arrive at our study site well before their major host, the Great Reed Warbler *Acrocephalus arundinaceus*, starts to breed (Jelınek V, Prochazka P, Pozgayova M, Honza M, pers. obs.), enabling them to synchronize egg-laying with the host species (Moskát *et al.* 2006). Moreover, host breeding starts gradually, with older birds breeding ahead of younger birds, reflecting a protracted arrival that can extend over 3–4 weeks (Jelínek V, Procházka P, Požgayová M, Honza M unpubl. data). This means that Cuckoos have an advantage over their hosts at the beginning of the nesting season. A similar pattern may also occur at the end of the breeding season, when the majority of Great Reed Warbler pairs have either already bred or are feeding nestlings; very few are initiating late replacement or second clutches, whereas Cuckoos are still present in similar numbers as at the beginning of the season. This uneven pattern of breeding (Fig. 1) provides us with the opportunity to assess whether a density-dependent relationship influences the probability of brood parasitism.

In light of the above-mentioned studies we predicted that the probability of parasitism would depend on the number of suitable host nests, with more nests available, resulting in a lower proportion being parasitized. We additionally predicted that a Cuckoo's nest-searching strategy would depend on host nest density. More specifically, predictors of brood parasitism (e.g. nest concealment or perch proximity) would be more important the greater the number of host nests available. To test these hypotheses, we extended a previous study by Moskát and Honza (2000) of a different heavily parasitized Great Reed Warbler population, with two main modifications. First, we used data from five consecutive years, and, secondly, we quantified host aggression to test for nest defence and the nesting cue hypothesis.

METHODS

This study was conducted between 20 April and 20 July 2008–2012 in two adjacent fishpond areas between Hodonín (48°51′N, 17°07′E) and Mutěnice (48°54′N, 17°02′E) in South Moravia, Czech Republic. The studied Great Reed Warbler

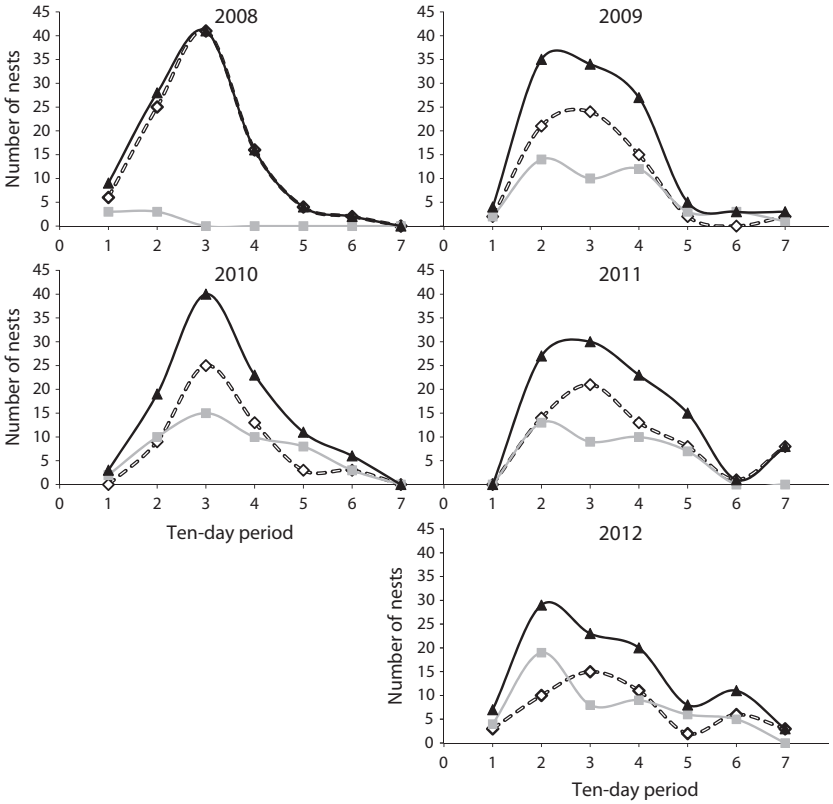

Figure 1. Number of nests which started (first egg laid) in 10-day periods over the five study years (first 10-day period begins on 1 May). Grey solid line – parasitized nests, white dashed line – non-parasitized nests, black solid line – all nests together).

population numbered 80–100 pairs and all individuals were marked with a unique combination of a standard aluminium ring and up to three coloured plastic rings. We systematically searched for nests in the littoral vegetation, which was dominated by the Common Reed *Phragmites australis*, with a smaller proportion of Narrow-leaved Cattails *Typha angustifolia* (hereafter referred to as reeds for both types of vegetation). We were able to find almost all nests each year thanks to regular mapping of male territories and checking for male mating status (Bensch 1996). Most nests were found during the building stage or at the beginning of egg-laying and were checked daily until clutch completion. Thereafter, the nests were checked less often (typically every 4 days), except for parasitized nests, which were checked daily to determine host response towards parasitic eggs. Each nest was tagged with a small piece of coloured tape and its location recorded with GPS. Eggs were numbered using a felt-tip pen according to laying order.

Nest and nest-site characteristics

Nest and nest-site characteristics were measured for almost all host pairs during the egg-laying period or incubation. Some nests were found late and had large nestlings or had been destroyed by predators before measurements could be taken (from 3% to 9% per year). In these cases, we measured only those nest and nest-site characteristics that remained intact. The following variables were recorded: laying date of the first egg (1 May = day 1), distance to the nearest tree serving as a potential Cuckoo perch (nearest shrub, tree or electric wire more than 5 m high), distance to nearest water's edge for the reed bed, distance to nearest active conspecific nest (measured from GPS positions), reed height above the water's surface, height of upper nest rim above water or ground level, height of vegetation above the nest, reed density (estimated as sparse, intermediate or dense), nest volume and Cuckoo nest view. The last variable was scored following the protocol of

Øien *et al.* (1996), i.e. direct – a Cuckoo sitting in a nearby tree can see the nest; indirect – the Cuckoo cannot see the nest directly but can locate it by activity of nesting birds; or no nest view – the nest is well hidden and the Cuckoo cannot see or locate it by activity of the nesting birds. Nest volume (V) was calculated as half an ellipsoid according to the formula: $V = 4/3(\pi \times a^2 \times b \times 1/2)$ where a = nest radius and b = nest height (Palomino *et al.* 1998). Both dimensions were obtained as the mean of two measurements of nest width and height. The underside of the nest usually terminated in loose tags of nesting material. As these contributed to the nest silhouette, nest height was measured from the nest rim to the end of these tags. Nest width was measured using callipers and all other measurements were obtained using a folding ruler. Distances to nearest potential perch site and the water's edge were assessed on the basis of previous training and checked with the assistance of aerial photos (http://www.mapy.cz). All measurements were collected by one person (V.J.), including scoring of Cuckoo nest view and reed density. We used the number of host nests available for Cuckoos (host nest density) as a measure of host breeding synchrony, considering a given host nest as available from the first day of egg-laying to the first day after the last egg was laid. As a typical Great Reed Warbler clutch in the study population was known to consist of five eggs (median = 5, mean ± sd = 4.65 ± 0.73, n = 333; unparasitized clutches from 2008–2012), this interval was set to 6 days. For each day within a season, we computed the number of host nests available for Cuckoos using the egg-laying dates of all nests found each year (i.e. not parasitized and unparasitized nests only as used in the following analyses). Host nest density for each nest was then expressed as the sum of these 'day nest values' over the 6-day interval when the nest was suitable for parasitism. This interval was shorter in nests depredated during the egg-laying phase.

Host aggression

In 2009 and 2010, we presented a stuffed Cuckoo dummy at host nests (both parasitized and unparasitized) and recorded aggressive behaviour. The experiment took place around the turn of the egg-laying and incubation stage, on average 3.6 days after clutch initiation (sd = 1.0, n = 78). The dummy was attached to a pole < 1 m from a focal nest and placed level with the nest rim. The behaviour of each member of the host pair was observed for 5 min from its first arrival from a distance of 10–15 m, after it had appeared within a 5-m diameter around the dummy. If there was no reaction and no bird was seen in the vicinity of the nest for 20 min from dummy exposure, the experiment was stopped and the dummy removed. Such nests were excluded from further analysis (seven nests from both years). The experiments were carried out between 08:00 and 20:00 h CET using one of three different Cuckoo dummies presented randomly. All experiments were carried out by M.P.

As a measure of host aggression, we used the sum of contact attacks on the dummy of both pair members, choosing this behavioural characteristic as it showed the highest level of individual variation in comparison with other traits (see also Trnka & Prokop 2012). Moreover, we considered this trait the most risky (in general) and, at the same time, the most effective behaviour for expelling Cuckoo females and preventing them from laying an egg.

Nest parasitism rates

Nests were considered as parasitized when they contained a Cuckoo egg or chick. Nests with a known uninterrupted egg-laying sequence, or those found later but with a complete clutch of four or five eggs, were classified as non-parasitized. All other nests were not considered for further analysis, except when they were used for calculation of host nest density (see above). We also included replacement clutches by the same females into our analyses, as Cuckoo females are able to choose between all active nests within their territories.

Parasitism rates differed markedly among the study years. In 2009–2012, more than 30% of nests were parasitized (2009 – 32%, 2010 – 47%, 2011 – 38%, 2012 – 50%), but only six of 100 nests (6%) were parasitized in 2008. This extremely low parasitism rate prevented us from using these data in the same way as data from the other 4 years; hence they were used only as a supplement for comparison with predicted patterns of brood parasitism. Data from 2009 to 2012 were pooled and analysed together (n = 404: 109, 93, 102, 100 nests in respective years).

Statistical analysis

All statistical analyses were performed with logistic regression within generalized linear models (GLM)

with a binomial error distribution and logit link function in R 2.15 (R Development Core Team 2012). Model simplification was performed through backward stepwise elimination of insignificant terms from the initial model based on change in deviance between the full and reduced models tested using a chi-square test (Faraway 2006, Crawley 2007). Comparisons between categorical predictor levels or their interactions in the minimum adequate model were performed using 'treatment' contrasts (Crawley 2007). All continuous predictors were centred (Schielzeth 2010) due to the inclusion of interaction terms. The initial model included nest parasitism (0 = nest unparasitized, 1 = nest parasitized) as a response variable, and host nest density, Cuckoo nest view, reed density, distance to nearest tree, distance to nearest water's edge, distance to nearest active conspecific nest, height of nest above water level, height of reed above the nest, nest volume and laying date as predictors. To test the hypothesis that Cuckoos change their nest-searching strategy in response to host nest availability, we included interactions between host nest density and all predictors, apart from laying date, into the model. The height of the reed was excluded from the initial model due to a strong correlation with the height of reed above the nest (r_S = 0.78).

The impact of host aggression on brood parasitism was tested for 71 nests over 2 years (2009 and 2010), 18 of which nests belonged to the same males. For this reason, we used generalized estimating equations (GEE; R package geepack; Yan 2002, Yan & Fine 2004, Hojsgaard *et al.* 2006) with a binomial error structure and independent correlation structure. Model selection was performed in the same manner as for GLM. The initial model included nest parasitism as a response variable, host nest density, number of attacks, reed density, nest status (monogamous, primary, secondary), laying date and three interactions as predictors, and male identity as a grouping variable. The first interaction was between reed density and number of attacks, as hosts may adjust aggressive behaviour based on the level of nest concealment. As Požgayová *et al.* (2013) found that polygynous males defend their nests less intensively compared with monogamous males, we also included interaction between nest status and number of attacks. Finally, to test whether the Cuckoo's nest-searching strategy depends on availability of host nests, we included the interaction between host nest density and number of attacks.

RESULTS

Seasonal host and parasite egg-laying patterns differed over the 5 years (Fig. 1). In 2008 and 2010, the number of nesting Great Reed Warbler pairs increased gradually, with a clear egg-laying peak in the third 10-day period of May followed by a similarly gradual decrease. In 2009, 2011 and 2012, the numbers of breeding pairs reached their maximum faster over at least two 10-day periods in May, followed by a rapid (2009), slow (2011) or moderate (2012) decrease.

The probability of brood parasitism increased with higher nest visibility and lower reed density, and decreased over the course of the breeding season (Table 1). Moreover, the interaction of

Table 1. The effect of nest and nest-site characteristics on the probability of brood parasitism in Great Reed Warbler nests in 2009–2012. Only the minimum adequate model from the logistic regression model analysis is presented. *P*-values of particular model terms are based on Type III sum of squares. *P*-values of differences between the levels of categorical predictors are in parentheses. Values for host nest density are not given because the presence of this term in the significant interaction prevents the reliable interpretation of this term.

Variable	χ^2	df	*P*	Estimate ± se
Intercept				–1.595 ± 0.626
Host nest density	–	–	–	—
Cuckoo nest view[a]*	24.04	2	< 0.001	1.673 ± 0.597 (indirect: *P* = 0.005)
				2.488 ± 0.638 (direct: *P* < 0.0001)
Reed density[b]*	6.67	2	0.036	–0.435 ± 0.274 (middle: *P* = 0.112)
				–0.884 ± 0.345 (dense: *P* = 0.011)
Laying date	7.70	1	0.006	–0.026 ± 0.009
Cuckoo nest view[a]* × Host nest density	7.84	2	0.019	0.169 ± 0.069 (indirect: *P* = 0.014)
				0.157 ± 0.073 (direct: *P* = 0.031)

*Categorical predictors with three levels (reference categories: no Cuckoo nest view[a] and sparse reed density[b]).

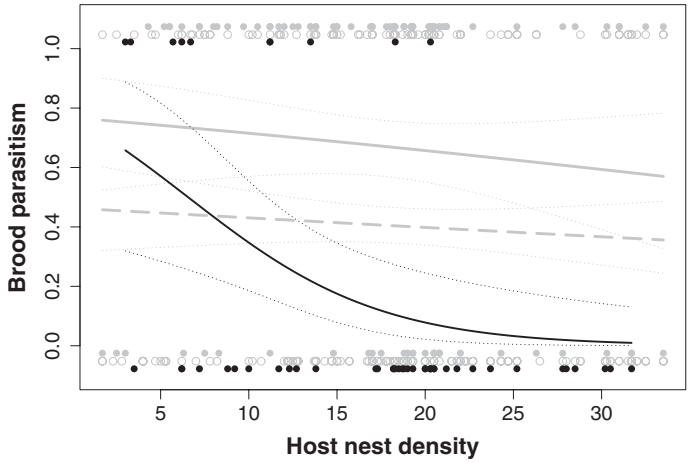

Figure 2. Relationship between the probability of brood parasitism and host nest density in Great Reed Warbler nests with different Cuckoo nest view in 2009–2012 (grey solid line and grey-filled circles – direct nest view, grey dashed line and grey open circles – indirect nest view, black solid line and black filled circles – no nest view). Dotted lines are 95% CIs. Predicted probabilities are based on simple logistic regression models. Points below zero represent unparasitized nests, points above one, parasitized nests; the symbols are depicted in separate lines to distinguish nests with different Cuckoo nest view.

Cuckoo nest view and host nest density was also found to be significant (Table 1). More specifically, the best-concealed nests (with no nest view) were likely to be parasitized at lower host densities, whereas they were quite safe at higher host densities. No such relationship was found for nests with indirect or direct Cuckoo nest view (Fig. 2).

During the nest defence experiments, 59 pairs attacked the Cuckoo dummy between two and 180 times, whereas 12 arriving pairs did not directly attack the dummy (mean number of attacks ± sd = 38 ± 38.2). Despite this variation, neither host aggression towards the Cuckoo nor any other variable except host nest density ($\beta \pm$ se = -0.069 ± 0.03, $\chi^2 = 4.52$, $P = 0.033$) had a significant effect on the probability of brood parasitism.

DISCUSSION

Here, we demonstrate for the first time that the number of simultaneously breeding host pairs significantly influences the probability of brood parasitism by a Cuckoo, and that the number of available host nests may modulate the Cuckoo's nest-searching strategy. Host pairs nesting during periods of high nest density were less parasitized than those nesting at lower densities. These results are similar to those of Martínez *et al.* (1996) and Clark and Robertson (1979) for other host–parasite systems.

In accordance with many other studies (e.g. Øien *et al.* 1996, Moskát & Honza 2000, Clarke *et al.* 2001, Avilés *et al.* 2009), we found that the best-concealed host nests (built in dense reed or those that were poorly visible with respect to Cuckoos) were at the lowest risk of brood parasitism. Accordingly, the optimal strategy to escape brood parasitism should be to build nests in such places and, in general, we confirmed this assumption. We also demonstrated that such a tactic proved useless when only a few host pairs were breeding simultaneously. More specifically, well-concealed nests were also parasitized at low host nest densities (Fig. 2) as Cuckoos could devote more time to searching for such nests, while ignoring them during periods of nest surplus. It appears therefore that Cuckoos adopt a strategy of finding as many host nests as possible. There are two possibilities why they should do so: first, finding enough host nests is so time-consuming that the Cuckoo must concentrate on locating only poorly hidden nests, and second, parasitic females pursue a strategy of locating as many host nests as possible to be able to select the most suitable nests, e.g. on the basis of egg colour matching (M. Honza *et al.* unpubl. data) or other characteristics (reviewed by Parejo & Avilés 2007). This latter possibility is in accordance with the finding of Nakamura *et al.* (2005), who showed that one Cuckoo female visited at least 16 host nests in her territory but parasitized only nine of them.

Consequently, the longer the hosts breed simultaneously in ample numbers, the higher the number

of pairs that have a chance of escaping parasitism by building their nests in less visible places, e.g. in denser vegetation and far from trees that offer the Cuckoo perches. In doing so, they gain an advantage over other pairs and increase their reproductive success despite the high overall parasitism rate in the population. Briskie *et al.* (1990) suggested a similar relationship at the interspecific level for American Yellow Warblers *Setophaga aestiva*, which were preferentially parasitized by Brown-headed Cowbirds over Least Flycatchers *Empidonax minimus*, whose nests were only used when nests of the primary host species became rarer.

In addition, our results showed a temporal pattern in parasitism pressure, with earlier nests parasitized more often than later nests. For example, when only six of 100 nests were parasitized in 2008, three of those were from the six earliest nests. Similarly, Welbergen and Davies (2009) found that the earliest nests of Eurasian Reed Warblers *Acrocephalus scirpaceus* suffered higher Cuckoo parasitism than later nests, a pattern also suggested by the data of Øien *et al.* (1998) for the same species. Nevertheless, it is hard to say what is behind this date-related effect. As stated above, in part it could be that Cuckoos have more time for nest searching at the beginning of the season; alternatively, as Eurasian Reed Warblers begin breeding on average 2 weeks later than the Great Reed Warbler, some Cuckoo females may switch host species later in the season. A further possibility is that Cuckoos preferentially parasitize earlier nests, as offspring in such nests have greater reproductive value than offspring that hatch later (e.g. Verhulst & Nilsson 2008, McKim-Louder *et al.* 2013).

Although distance to nearest perch site is generally regarded as an important predictor of brood parasitism in both cuckoo (Alvarez 1993, Moskát & Honza 2000, Antonov *et al.* 2007, Welbergen & Davies 2009) and cowbird hosts (e.g. Clotfelter 1998, Hauber & Russo 2000, Patten *et al.* 2006), we did not confirm such a relationship. In agreement with Moskát and Honza (2000) and Antonov *et al.* (2007), we also found no effect of habitat edge on brood parasitism, despite such a relationship being substantially supported in the cowbird–host system (Patten *et al.* 2011). Finally, similarly to Moskát & Honza (2000) and Avilés *et al.* (2009), we were also able to show that nest size did not predict probability of brood parasitism (but see McLaren & Sealy 2003).

It is surprising that the influence of host aggression on probability of brood parasitism has been tested relatively rarely compared with the effect of nest-site characteristics, despite aggressiveness of host species generally increasing with vulnerability to brood parasitism (Moksnes *et al.* 1991, Røskaft *et al.* 2002). Furthermore, populations of some host species living in sympatry with brood parasites have been shown to display higher aggression to dummies than populations living in allopatry (Burhans *et al.* 2001, Røskaft *et al.* 2002). Despite results indicating that host aggressiveness towards brood parasites is associated with nest parasitism, we know almost nothing about its effectiveness. We found no relationship between host aggression towards the Cuckoo dummy and probability of brood parasitism. It would appear therefore that although our host species is very aggressive and vigorously attacks enemies near its nest (Molnár 1944, Janisch 1948–51, Bártol *et al.* 2002, Požgayová *et al.* 2009), it is unable to prevent Cuckoo females from laying eggs in the nest. Nakamura *et al.* (2005) reported that a female Cuckoo laid an egg into the nest of an Oriental Reed Warbler *Acrocephalus orientalis* at the ninth attempt, despite always being attacked by up to four Warblers. Similarly, host aggressiveness does not prevent brood parasitism in several cowbird host species (Gill *et al.* 1997, Olendorf & Robinson 2000). However, Welbergen and Davies (2009) have shown a strong correlation between local parasitism risk and mobbing propensity in the Eurasian Reed Warbler, with mobbers in areas of high parasitism risk suffering a more than 20% lower parasitism rate. This is surprising as mobbing in this small-bodied host is based mainly on alarm calls (Welbergen & Davies 2008, Čapek *et al.* 2010) and heavier and much more physically aggressive Great Reed Warblers were unable effectively to protect their clutches. We believe that Eurasian Reed Warblers may be able to avoid Cuckoo parasitism using another method. Previous studies have shown that some Cuckoo hosts, including the Eurasian Reed Warbler, tend to reject model eggs if a Cuckoo dummy is presented before experimental parasitism (Davies & Brooke 1988, Moksnes & Røskaft 1989) and it may be this that helps explain the Cuckoo's unwillingness to parasitize the better guarded nests of Eurasian Reed Warblers.

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Kapitola 2

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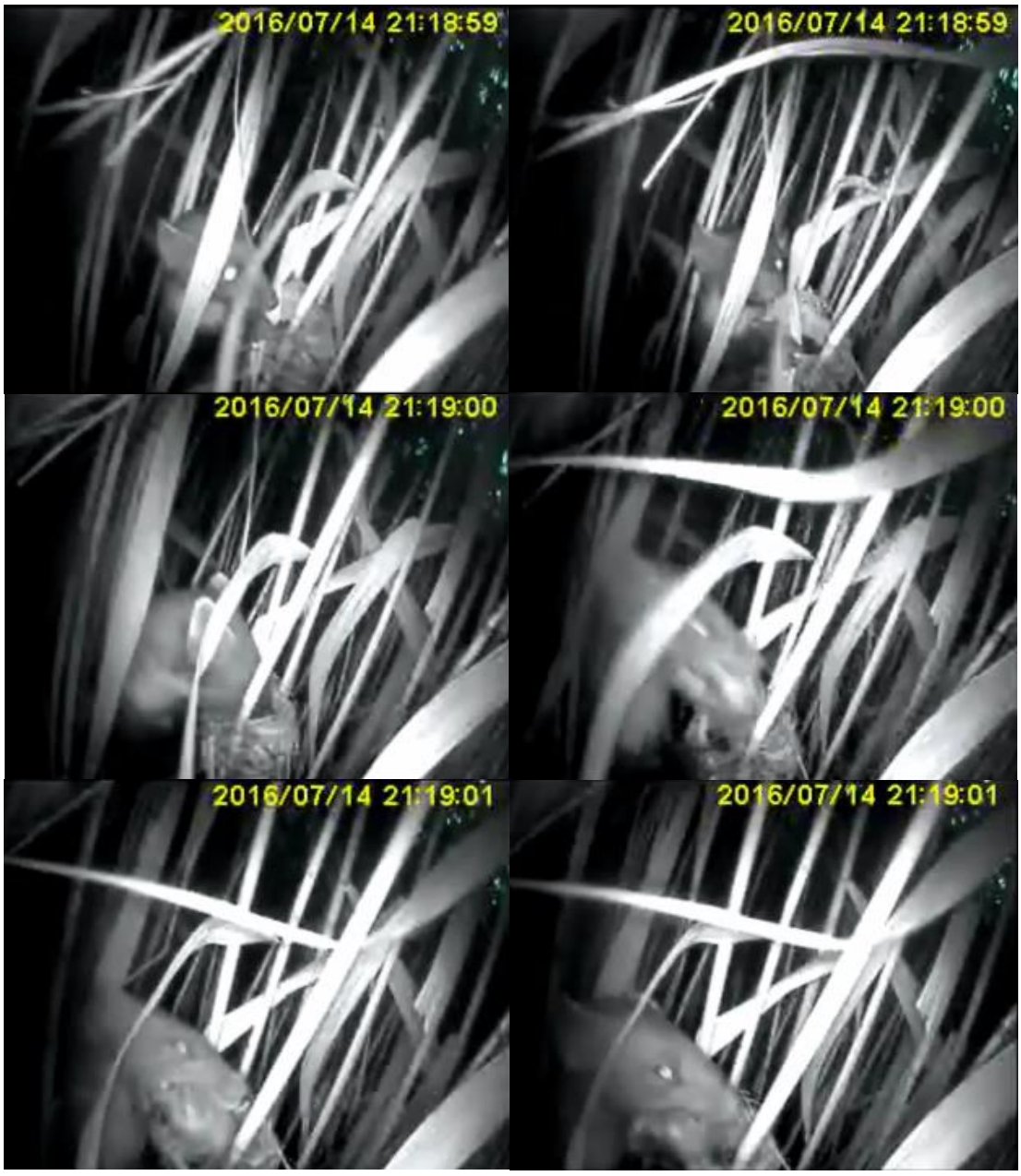

Záznam predace hnízdo rákosníka obecného (*Acrocephalus scirpaceus*) s šestidenním mládětem kukačky obecné (*Cuculus canorus*) kunou lesní (*Martes martes*).

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ORIGINAL ARTICLE

Do common cuckoo chicks suffer nest predation more than host nestlings?

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Abstract
Nestlings of brood parasites exhibit more intensive begging than offspring of their hosts to gain sufficient amount of food or competitive advantage over host nestlings. This begging behaviour should be costly because exuberant acoustic begging may more likely attract nest predators. However, to date, nobody has explored the survival of nests with and without chicks of brood parasites in the common cuckoo (*Cuculus canorus*) host system. Here, we analysed an extensive dataset of 817 great reed warbler (*Acrocephalus arundinaceus*) and 788 reed warbler (*Acrocephalus scirpaceus*) nests to explore the relationships between nest predation and parasitism status (parasitized vs. non-parasitized), nest contents (cuckoo chick vs. host nestlings) and age of nestlings. We found that although parasitized nests had higher predation rate than non-parasitized nests in the incubation stage, the effect of original parasitism status almost disappeared in the nestling stage. In both host species, nests with younger cuckoo chicks survived similarly to nests with host nestlings of the same age (till the ninth day of age). Later on, however, nest contents influenced nest predation in each species differently. While nests with older cuckoo chicks (from the ninth to the 17th day of age) did not survive worse that host nestlings in the great reed warbler, older cuckoos survived much worse than host nestlings in reed warbler nests. Finally, nest survival decreased with nestling age in all three species. Thus, it seems that common cuckoo chicks can be penalized for more intensive begging only in nests of smaller reed warbler hosts.

Significance statement
Parental feeding of young is in birds frequently accompanied by striking nestlings begging behaviour serving as a signal of their need. Brood parasites exhibit even more intense food solicitation than their hosts which may attract predators to the nest. However, this hypothesis has never been tested in a widely studied brood parasite species—the common cuckoo. Here, we analysed survival of more than 1600 nests of its two main host species. We found that nests containing older common cuckoo chicks were depredated more frequently than nests with host own nestlings only in the smaller reed warbler hosts but not in the larger and more aggressive great reed warblers. This shows that the intensity of begging could be costly in terms of nest predation at least in some common cuckoo host species.

Keywords Brood parasitism · Great reed warbler · Nest survival · Reed warbler

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Introduction

The common cuckoo (*Cuculus canorus*, hereafter cuckoo) is an obligate brood parasite that lays eggs in the nests of numerous host species and relinquishes the whole parental care to them. The cuckoo chick avoids future competition with host offspring by evicting the host progeny soon after hatching, whereby it monopolizes the entire parental care of its hosts

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(Wyllie 1981; Davies 2000). The vast majority of cuckoo host species are notably smaller (typical host weight is about 15 g, the cuckoo being approximately eight times heavier; Davies 2000). This simple fact posits a greater overall feeding effort of foster parents because the parasitic chick is bigger than the whole host brood and fledges later than host nestlings (Grim 2006). It is possible that both these factors (amount and length of care) may influence host decision whether to terminate a given nesting attempt due to physiological changes, such as exhaustion (Holen et al. 2001) or unusually long nestling period (Grim et al. 2003; Grim 2007). Thus, the cuckoo chick has to adequately stimulate the foster parents to cover its considerable needs.

The enhanced level of acoustic solicitation of cuckoo chicks compared to hosts was reported (Davies et al. 1998; Kilner and Davies 1999; Butchart et al. 2003) especially in later stages of its development when cuckoo call rate can reach approximately 1.5 times the call rate of a whole host brood of the same age (Kilner and Davies 1999; Butchart et al. 2003). Moreover, this difference seems to increase in the course of time (Kilner and Davies 1999; Butchart et al. 2003; MH and PP unpublished results). The non-acoustical begging by wing-shaking is also more conspicuous in cuckoos than in their hosts (Grim 2008). In contrast to their hosts, cuckoo chicks also frequently exhibit acoustic solicitation when parents are absent (Šicha et al. 2007). Similarly, to the cuckoo, also other brood parasite species (Redondo 1993; Briskie et al. 1994; Dearborn 1999; Soler et al. 1999; Redondo and Zuñiga 2002) exhibit more intense acoustic begging.

It was experimentally shown that parents respond to more frequent begging calls by delivering more food to nestlings (Kilner et al. 1999) and that a more intensely soliciting nestling is preferred to its less demanding siblings (Dearborn 1998). Hence, it should be profitable for the brood parasites to exhibit more intense begging behaviour than their hosts. Nonetheless, according to Zahavi's (1975) handicap principle if the begging serves as a signal of offspring need, it must be costly to produce (Maynard-Smith and Harper 2000).

In the case of begging behaviour, two costs ensuring the signal honesty were suggested, the metabolic cost of higher energetic expenditure during signalling and the predation cost of greater danger of finding the nest by predators due to nestling loud vocalization. The energetic cost is considered as almost negligible (Soler et al. 1999; Chappell and Bachman 2002; Leonard et al. 2003; but see Kilner 2001) or at least manifested only in some species (Rodríguez-Giroñés et al., 2001). Thus, the enhanced risk of predation should be the major force determining the intensity of begging behaviour. Indeed, experimental studies consistently showed that artificial nests with broadcasted begging calls were depredated more frequently than silent controls (Haskell 1994; Leech and Leonard 1997; Dearborn 1999; Haskell 1999; McDonald et al. 2009). More interestingly, McDonald et al. (2009) showed that white noise pulses enhanced the risk of predation to the same level as real begging calls. Similarly, long lasting mobbing calls played back during the day near nest boxes may enhance the probability of nest predation by nocturnal mammalian predators (Krams et al. 2007). Finally, Haff and Magrath (2011) directly observed the attraction of predators to active nests by playing back the nestling begging calls at these nests.

Nonetheless, the real magnitude of the predation cost could not be assessed by these studies because in all of them except for McDonald et al. (2009); the acoustic signals were broadcasted at abnormally high or unnatural levels. Moreover, these experimental studies inherently exaggerated the predation cost because they completely neglected the fact that begging behaviour is exhibited by nestlings mostly in situations when the parents are at the nest, indicating that it is safe to beg. When the danger is really at hand, nestlings of hosts (Davies et al. 2004; Platzen and Magrath 2004) and brood parasites (Madden et al. 2005; Davies et al. 2006) crouch or become silent in response to alarm calls of their parents or odd movements of neighbouring vegetation (Haff and Magrath 2010). These behavioural adaptations may markedly lower the real predation cost of begging even in the case of intensely begging brood parasites as hypothesised by Davies (2011). A possible option partly resolving the problem that nestlings beg mostly in safe moments is an experimental transfer of more intensively begging brood parasite chicks into non-parasitized nests of their hosts and studying predation in such nests. Ibáñez-Álamo et al. (2012) indeed found that experimental nests with a cross-fostered great spotted cuckoo (*Clamator glandarius*) chick were significantly more depredated than control nests containing only blackbird (*Turdus merula*) nestlings.

In our study, we explored the nest survival of two common cuckoo host species: the reed warbler (*Acrocephalus scirpaceus*, hereafter "RW") and the great reed warbler (*Acrocephalus arundinaceus*, hereafter "GRW") in relation to whether the nests were parasitized by the cuckoo or not (hereafter parasitism status). We analysed nest survival in natural conditions when begging (generally less intense than in playback experiments) is exhibited in concert with antipredation behaviour of parents and nestlings, lowering thus the probability of nest detection (Davies et al. 2004, 2006; Platzen and Magrath 2004). If begging enhances the risk of nest predation, cuckoo chicks will be more frequently predated than host nestlings.

However, an inherent problem with this kind of approach is the presence of a correlation between the probability of brood parasitism and nest site characteristics because the cuckoo females preferentially parasitize less concealed nests (e.g. Øien et al. 1996; Moskát and Honza 2000; Jelínek et al. 2014) and such nests should be consequently more frequently depredated. We tried to resolve this problem by using a partially natural experiment where in some parasitized nests parasitic eggs were either ejected or did not hatch, while in other

nests, we cross-fostered the cuckoo chicks shortly after hatching for the purpose of other studies (Fig. 1). As a result, we were able to indirectly investigate whether the potential difference in nest predation was better explained by nest site characteristics i.e. easier detectability of less concealed parasitized nests (which was not quantified directly in our study) or by the actual presence of a cuckoo chick in those nests.

More specifically, we firstly explored the role of parasitism status in nest survival during incubation when there is no difference between parasitized and non-parasitized nests in terms of nestling or parents' behaviour. We predicted that daily survival rate of parasitized host nests would be lower than daily survival rate of more concealed (e.g. Jelínek et al. 2014) non-parasitized nests. Secondly, owing to the higher begging activity of older cuckoo chicks (Kilner and Davies 1999; Butchart et al. 2003; MH and PP unpublished results), we predicted that nests containing older cuckoo chicks should suffer from higher predation than nests containing host nestlings while the survival of nests with host nestlings and younger cuckoo of the same age would not differ. And thirdly, because the intensity of begging increases with the nestling age (Kilner et al. 1999), we predicted a corresponding decrease in daily survival rates in all three species.

Methods

The study was conducted between 20 April and 31 July 2008–2015 in two adjacent fishpond areas between Hodonín (48° 51′ N, 17° 07′ E) and Mutěnice (48° 54′ N, 17° 02′ E) in South Moravia, Czech Republic. We systematically searched for nests in the littoral vegetation dominated by the common reed (*Phragmites australis*), with a smaller proportion of the narrow-leaved cattail (*Typha angustifolia*). Each nest was tagged with a small piece of coloured tape and its location recorded with GPS. Eggs were numbered using a felt-tip pen according to laying order to reveal missing eggs.

The population of GRW numbering 80–100 pairs was individually marked and systematically studied during the whole period. We were able to find almost all nests each year thanks to regular mapping of male territories and checking for male mating status (Bensch 1996). Most nests were found during the building stage or at the beginning of egg laying and were checked daily until clutch completion. Thereafter, the nests were checked less often (typically every 4 days, mean number of visits per day ± SE = 0.328 ± 0.009 during the incubation period), except for parasitized nests, which were checked daily or every second day for the first 5 days of incubation to determine host response towards parasitic eggs (mean number of visits per day ± SE = 0.414 ± 0.012). Reed warblers breed in the locality in higher numbers (200–300 pairs); nonetheless, we studied them less intensively than GRW depending on particular research questions. Thus, during 2008 and 2009, the number of RW nests we found was low and these nests were checked with insufficient frequency. From 2010 onwards, we found ample numbers of RW nests; hence, we analysed RW nest survival data from these six seasons (2010–2015). RW nests were typically found later (often during incubation) and checked with a similar frequency as GRW nests (mean number of visits per day ± SE = 0.345 ± 0.011 for non-parasitized nests and 0.407 ± 0.033 for parasitized nests). The influence of nest

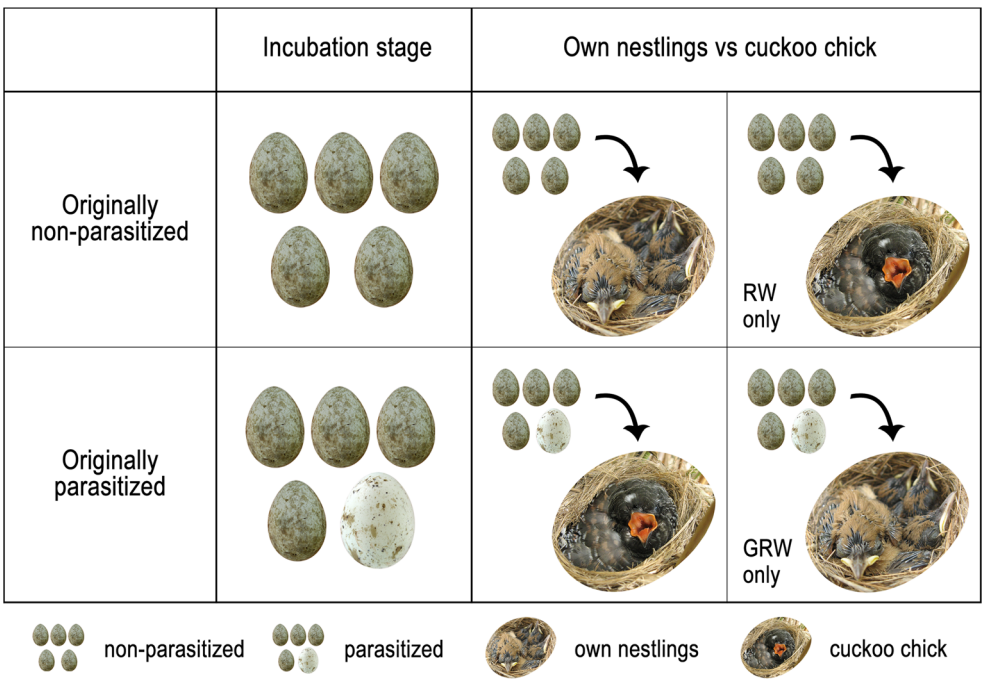

Fig. 1 Groups of great reed warbler (*GRW*) and reed warbler (*RW*) nests according to parasitism status and actual nest contents (parasitism group) in each nest survival analysis (parasitism groups in both analyses concerning host nestlings and younger or older cuckoos did not differ). Cuckoo eggs were either ejected or did not hatch in parasitized nests with own nestlings. Cuckoo chicks were cross-fostered shortly after hatching in non-parasitized nests with cuckoo chicks. Most groups of nests pertain to both host species, except for those indicated. For sample sizes see Table 1

checks on the nest survival of open-nesting songbirds was subject of several studies. Most of them showed no (Götmark 1992; O'Grady et al. 1996; Mayer-Gross et al. 1997; Ortega et al. 1997; Weidinger 2008) or even a positive short-term (Weidinger 2008) effect of repeated nest visitation on nest survival. Thus, we believe that small differences in nest visitation rate between parasitized and non-parasitized nests representing only 1.03 visit during a standard 12-day-long incubation in GRW and 0.74 visit in RW can hardly influence nest survival to the degree that would change our conclusions. In fact, a positive effect of visitation frequency, if present also in this study, would make the finding of predicted higher predation on parasitized nests conservative. We did not collect data blind because it was not needed in our kind of study.

Nests of both species are regularly parasitized by the cuckoo at our study site (Table 1). Cuckoo females locate host nests mostly during nest building and subsequently lay their eggs (Wyllie 1981). During egg-laying, cuckoos successively remove up to four host eggs (Gärtner 1981) and thus lower the reproductive success of their hosts even in cases when these eject the parasitic egg. Moreover, the cuckoo is also a nest predator and it frequently partially (Moksnes et al. 2000) or exceptionally completely (Wyllie 1975; Gärtner 1981) depredates host clutches. Previous research showed that of 53 RW nests filmed during egg-laying stage 14 were successfully parasitized by the cuckoo and in six nests the cuckoo only partially predated the nest contents. No case of removing own eggs by the reed warbler was registered (Moksnes et al. 2000). Moreover, we found a positive correlation between the annual number of parasitized GRW nests and the annual proportion of non-parasitized GRW nests with missing eggs during egg laying ($r_p = 0.70$, df = 6, $p = 0.05$). Thus, we consider as parasitized by definition each host nest where we recorded parasitic egg or missing host eggs in laying sequence because they were probably discovered by cuckoos regardless whether they were successfully parasitized ($n = 294$ and 59 for GRW and RW, respectively) or only partially depredated ($n = 53$ and 10 for GRW and RW, respectively). We consider as parasitized also those host nests found with unusually low number of eggs (two- or three-egg clutches in GRW, $n = 9$ for both groups; and two-egg clutches in RW, $n = 3$) in May and the first half of June (natural two- or three-egg clutches appear from the second half of June; VJ, PP unpublished results). In these nests, we had also additional evidence which led us to classify them as "parasitized", such as when there was a replacement clutch of a particular female with more eggs than in the first breeding attempt or there were signs of disturbance in the nest (traces of yolk or white in nest cup etc.). The rest of host nests were classified as non-parasitized except for three GRW nests which could not be assigned to any group because of our

Table 1 Effective sample sizes and numbers of all and depredated parasitized and non-parasitized great reed warbler and reed warbler nests in each nest survival analysis (effective sample size = number of survived nest days + number of observation intervals during which a nest was depredated)

		Great reed warbler			Reed warbler		
		Number of nests	Depredated	Effective sample size	Number of nests	Depredated	Effective sample size
Incubation stage							
Overall		793	74	8322	723	114	6032
Non-parasitized		430	27	4670	651	95	5499
Parasitized		363	47	3652	72	19	533
Host nestlings vs. younger cuckoo							
Overall		678	47	4299	567	44	3370
Non-parasitized	Own nestlings	382	29	2405	477	33	2804
	Cuckoo	7[a]	0	–	45	4	314
Parasitized	Own nestlings	146	9	961	6[a]	2	–
	Cuckoo	143	9	933	39	5	252
Host nestlings vs. older cuckoo							
Overall		663	56	4191	557	50	3252
Non-parasitized	Own nestlings	382	29	2405	477	33	2804
	Cuckoo	6[a]	0	–	38	7	265
Parasitized	Own nestlings	146	9	961	6[a]	2	–
	Cuckoo	129	18	825	37	9	183

Cuckoo eggs were either ejected or did not hatch in parasitized nests with own nestlings. Cuckoo chicks were cross-fostered shortly after hatching in non-parasitized nests with cuckoo chicks. For the more details please see Methods section

[a] Nests excluded from analyses due to the small sample size

mistakes when recording the data (three GRW nests) and were excluded from all analyses.

The type of data used in the present study inherently has a certain level of ambiguity as the exclusion of a particular group of nests led by an effort to exclude some type of bias could at the same time introduce another bias. For example, classification of nests with missing host eggs in laying sequence as non-parasitized (no cuckoo egg was detected in the nest) would lower survival of "truly" non-parasitized nests and increase survival of "truly" parasitized nests. The exclusion of these nests from analyses would, however, increase survival of "truly" parasitized nests. Thus, we classified all GRW and RW nests on the basis of our best knowledge and experience according to the above mentioned criteria to achieve the most realistic results. If we falsely classified some non-parasitized nests as parasitized, it would bias results in an opposite direction with regard to our predictions. The classification we used hence makes our conclusions conservative.

Stages of the breeding cycle and nest fate

We classified the fate of nests into three categories. Successful nests survived (at least one egg hatched or one nestling survived) the particular stage of the breeding cycle (see below). Nests whose whole contents were missing before the ninth or the 17th day of the nestling or old cuckoo stage (see below), respectively, were classified as depredated. A relatively high number of nests (54, 18 and 11 GRW; 50, 9 and 6 RW nests in incubation, nestling and old cuckoo stage, respectively) were abandoned for various reasons but were not predated (e.g. brood parasitism in incubation stage, due to adverse weather, starvation or illness). Even though these nests were neither successful nor depredated (as defined above), we included them into the analysis as successful because they could be subject to nest predation before the desertion took place. The exposure time of these nests was censored by the last control when the nest was still active.

We divided the breeding cycle into four stages (egg laying, incubation, nestling and old cuckoo) differing in nest contents or frequency of parental visits (Kilner et al. 1999). The egg-laying stage was considered as a time period between the laying of the first and the last egg. Because the ordinary clutch of GRW and RW numbers 4–6 and 3–5 eggs, respectively (VJ, PP unpublished data), this stage lasts up to 5 days. Both host species discriminate cuckoo eggs and reject them by ejection or desertion of the whole clutch. Because of this behaviour, it is difficult to determine whether the rare predation events during egg laying (29 of 793 GRW and 15 of 464 RW nests) took place in still active or already abandoned nests. It is also possible that hosts destroyed all eggs during the ejection of a cuckoo egg, or that a cuckoo ate the whole incomplete clutch during host egg laying, however, did not lay its egg. For all these reasons, the uncertainty in determining the reason of nest loss during egg laying is very high and we thus excluded this stage from our analyses.

The incubation stage lasted from the day of laying the last egg to the day when the first nestling hatched. The length of incubation varies (from 10 to 15 days) depending on the nest contents (cuckoos hatch markedly earlier) or other unknown circumstances (e.g. weather condition). If we did not check the nest on the day of hatching, the last day of incubation was estimated from the stage of nestling development.

We defined the nestling stage as an 8-day interval between the hatching day of the first nestling (first day of age = the day of hatching) and the ninth day of its age. However, the exposure time of each nest during the nestling stage was not equal in all nests. This was because the last day when we checked the nest contents (especially in RW) was mostly the day when we ringed nestlings (between the sixth and the ninth day of age). If a nest survived till the ninth day, we considered it as successful as we did with other nests which were last checked as active before this time. Thus, the exposure time of the nestling stage was 8 days (from the first to ninth) for nests which were last checked on the ninth day of age, 7 days for nest which were last checked on the eighth day of age etc. Because we usually did not check nests after the ringing, we did not take into consideration any occasional controls after the ninth day of age. This is the reason why we considered a small number of nests depredated or deserted after the ninth day of age as successful by definition.

As cuckoo chicks stay in the nest for a longer time than host nestlings, we divided the nestling period of cuckoo chicks into two stages. The first one corresponds with the nestling stage of host nestlings—"younger cuckoo" (from the first to the ninth day of age) which enabled us to compare the survival between nests containing host nestlings and cuckoo chicks. To ensure the direct comparability of nests containing host nestlings and younger cuckoo chicks, we set the last positive control of nests with cuckoo chicks in the same manner as in nests with host nestlings (ignoring the controls after the ninth day of age). Otherwise (division of the whole cuckoo nestling period using a fixed criterion of the ninth day), all successful nests with cuckoos would have 8-day-long exposure time while the exposure time of nests with host nestlings would differ in each nest (see above). The second part of cuckoo nestling period—the "older cuckoo" stage started on the ninth day of age and lasted to the 17th day of age which corresponds to the first day when cuckoos fledged from RW nests (in GRW they fledged about 3 or 4 days later). We treated the 17th day of the older cuckoo stage in the same manner as the ninth day of the nestling period (see above).

Statistical analysis

We modelled daily nest survival rates in MARK 6.1 (White and Burnham 1999) and evaluated the support for each model

by using an information–theoretic approach (Burnham and Anderson 2002). Analyses of nest survival were performed for each host species and each stage of the breeding cycle separately to evaluate the specific hypothesis. The incubation and nestling datasets comprised data from all years for both host species (8 and 6 years for GRW and RW, respectively).

To evaluate the specific hypotheses, we established a restricted number of biologically sensible candidate models. Each model included year (nominal variable) and date (continuous variable) as covariates and combinations of specific predictors for each dataset.

At the incubation stage, we evaluated whether parasitized nests are more vulnerable to nest predation than non-parasitized ones. Thus, we had only two candidate models (with and without parasitism status as a nominal predictor). We did not include nest age as a predictor of nest survival at the incubation stage to keep the models simple. This is well justified because in contrast with the nestling stage (see below) eggs do not change their appearance during incubation in a way that would be relevant to their conspicuousness for predators.

At the nestling stage, we investigated the effect of nest contents (cuckoo or host nestlings) and nestling age (continuous predictor measured in days) on nest predation. Because nests containing cuckoo chick are always parasitized in natural conditions, it would not be possible to ascribe the potential differences in nest predation to parasitism status or to the presence of cuckoo chick in the nest. Fortunately, the presence of originally parasitized nests where host nestlings were raised (e.g. after ejection of the cuckoo egg or when the cuckoo chick did not hatch) as well as originally non-parasitized nests where a cuckoo chick was experimentally added shortly after hatching, allowed us to control our results for this fact. Accordingly, we established four groups of nests: (i) originally parasitized nests containing a cuckoo chick, (ii) non-parasitized nests with host nestlings, (iii) originally parasitized nests with host nestlings and (iv) non-parasitized nests with a cuckoo chick (Fig. 1; for sample sizes, see Table 1). As we had only seven originally non-parasitized GRW nests with experimentally added cuckoo chick, we excluded them from the dataset. Similarly, in the RW, the low parasitism rate combined with low cuckoo egg ejection by the RW (only 4 of 68 cuckoo eggs ejected) forced us to exclude the group of parasitized nests with host nestlings (n = 6). For these reasons, we could not analyse parasitism status and nest contents as a 2 × 2 factorial design. Instead, we created a new combined categorical predictor (parasitism group) with three levels where each level represents one of the three remaining groups of nests, characterizing both the parasitism status and nest contents.

To compare the predation of host nestlings with cuckoo chicks, we performed two separate analyses. Firstly, we compared survival of nests containing host nestlings and younger cuckoo chicks during the nestling stage (from the first to ninth day of age). Secondly, as the differences in begging and appearance on the nest between host nestlings and cuckoo chicks occur later (when older cuckoo chicks beg more intensely), we compared survival of nests containing host nestlings during the nestling stage (from the first to the ninth day of age) with nests containing older cuckoos (from the ninth to the 17th day of age).

The candidate models for the nestling stage comprised models with covariates (date and year, see above) and all combinations of two predictors: parasitism group and age (as a time–dependent variable). We thus gained four candidate models (Table 2). The same four models were used in the second analysis comparing survival of host nestlings and older cuckoo chicks.

All candidate models were built without standardizing covariates and predictors and with log–link function (Dinsmore et al. 2002). We used the Akaike's information criterion corrected for small sample sizes (AIC_c) and the associated Akaike weights (w_i) to evaluate support for each model within the set of candidate models. When no model was clearly the best ($w_i > 0.90$), we averaged the whole set of candidate models according to the procedure of Burnham and Anderson (2002). Where applicable, we present these resulting average models and the daily survival rates obtained from these average models.

Results

During the eight consecutive breeding seasons (six for RW), we found more than 900 nests of both species. Of these, 817 GRW and 788 RW nests were active and contributed at least one exposure nest day to our nest survival analyses (Table 1).

Incubation stage

Models containing parasitism status gained the best support ($w_i = 0.97$ in GRW and $w_i = 0.65$ in RW), although in RW both models (with and without parasitism status) explained data similarly ($\Delta AIC_c = 1.20$; Table 2). In both species, parasitized nests had lower daily survival rate than non-parasitized nests although this relationship was somewhat weaker in the RW as 95 % confidence intervals (CI) for the parameter estimate comprised zero (Table 3).

Host nestlings vs younger cuckoo

No model explaining nest survival at the nestling stage gained substantial support in either host species ($w_i \leq 0.58$, Table 2). Model averaging showed that age of nestlings was an important predictor of daily survival rate of GRW and RW nests. As predicted, the probability of survival decreased with age in both host and cuckoo chicks (Table 3) and nests containing

Table 2 Models predicting daily survival rates of great reed warbler and reed warbler nests in each nest survival analysis

Analysis	Model	w_i	AICc	ΔAICc	*K*	Deviance
Great reed warbler						
Incubation stage	int. + date + year + parasitism	0.97	662.46	0	10	642.43
	int. + date + year	0.03	669.33	6.86	9	651.30
Host nestlings vs. younger cuckoo	int. + date + year + age	0.53	429.35	0	10	409.30
	int. + date + year + parasitism group + age	0.42	429.83	0.48	12	405.76
	int. + date + year	0.03	435.21	5.86	9	417.17
	int. + date + year + parasitism group	0.02	436.24	6.89	11	414.18
Host nestlings vs. older cuckoo	int. + date + year + age	0.62	489.25	0	10	469.20
	int. + date + year + parasitism group + age	0.37	490.28	1.03	12	466.21
	int. + date + year	0.01	497.73	8.48	9	479.69
	int. + date + year + parasitism group	0.01	497.97	8.72	11	475.91
Reed warbler						
Incubation stage	int. + date + year + parasitism	0.65	782.86	0	8	766.83
	int. + date + year	0.35	784.06	1.20	7	770.04
Host nestlings vs. younger cuckoo	int. + date + year + age	0.58	360.71	0	8	344.67
	int. + date + year	0.19	362.94	2.22	7	348.90
	int. + date + year + parasitism group + age	0.17	363.19	2.48	10	343.12
	int. + date + year + parasitism group	0.07	365.00	4.29	9	346.95
Host nestlings vs. older cuckoo	int. + date + year + parasitism + age	0.86	388.87	0	10	368.81
	int. + date + year + parasitism	0.14	392.86	3.98	9	374.47
	int. + date + year + age	0.00	400.18	11.30	8	384.13
	int. + date + year	0.00	404.71	15.83	7	390.67

See Methods section for definition of model covariates and predictors

Deviance difference between each model and the saturated model in −2 log likelihood, *ΔAICc* difference between each model and the top model in Akaike's information criterion corrected for small samples (AICc), *K* number of parameters in the model, w_i Akaike weight, a measure of each model's relative support within the set of candidate models, *int.* intercept

younger cuckoo chicks did not survive worse than those containing host nestlings in both host species (Figs. 2 and 3).

Host nestlings vs older cuckoo

Also, when we compared survival of nests with host nestlings and nests with older cuckoos (from ninth to the 17th day of age), no model was clearly the best in either host species ($w_i \leq 0.86$, Table 2); however, the results differ markedly between GRW and RW hosts. In the GRW, the results remained qualitatively the same as in the previous analysis—model averaging showed that parasitism group was not an important predictor of nest survival. However, in the RW, parasitism group was clearly the best predictor (Table 2). Here, nests containing older cuckoos survived worse than nests with host nestlings although this relationship was a little bit weaker in non-parasitized nests with older cuckoos where 95 % CI for the parameter estimate comprised zero (Table 3). Model averaging also showed that nestling age was an important predictor of nest survival in both host species (Table 2). As predicted, the probability of survival decreased with age (Table 3).

Discussion

The four main conclusions of our study are (i) parasitized nests were more prone to depredation during the incubation stage, (ii) predation of host nestlings and younger cuckoo chicks of the same age did not differ, (iii) older cuckoo chicks survived worse than host nestlings in RW nests but not in GRW nests, (iv) the probability of nest predation increased with nestling age. More importantly, the majority these findings (except iii) were qualitatively the same for two different cuckoo host species: great reed warbler and reed warbler.

The reason why the parasitized nests suffered higher predation during the incubation stage could be simply because cuckoos preferentially parasitized nests placed in sparser vegetation (Moskát and Honza 2000; Jelínek et al. 2014) and these more conspicuous nests could be subsequently easier to find also by nest predators. In this case, cuckoos would thus select nests which are more prone to be depredated. Alternatively, the predator responsible for increased predation of parasitized nests could be the cuckoo itself. Cuckoo females eat up to four eggs prior to the parasitism event (Gärtner 1981; Moksnes et al. 2000); however, the predation of the whole

Table 3 Parameter estimates, standard errors (SE) and 95 % confidence intervals (CI) for each term in average models predicting daily survival rates of great reed warbler and reed warbler nests in each nest survival analysis

Analysis	Term	Estimate ± SE	LCI	UCI
Great reed warbler				
Incubation stage[a]	Intercept	4.31 ± 0.45	3.42	5.20
	Date	0.021 ± 0.010	0.0005	0.0408
	Parasitism[b]	−0.76 ± 0.26	−1.27	−0.25
Host nestlings vs. younger cuckoo	Intercept	5.50 ± 0.67	4.20	6.82
	Date	0.003 ± 0.012	−0.021	0.028
	Par. with cuckoo[c]	0.60 ± 0.41	−0.19	1.40
	Par. with own nestlings[c]	0.61 ± 0.40	−0.18	1.40
	Age	−0.22 ± 0.08	−0.38	−0.07
Host nestlings vs. older cuckoo	Intercept	5.60 ± 0.63	4.36	6.84
	Date	0.001 ± 0.011	−0.021	0.023
	Par. with cuckoo[c]	−0.27 ± 0.32	−0.90	0.37
	Par. with own nestlings[c]	0.44 ± 0.40	−0.34	1.22
	Age	−0.23 ± 0.07	−0.37	−0.08
Reed warbler				
Incubation stage[a]	Intercept	3.58 ± 0.42	2.75	4.41
	Date	0.012 ± 0.009	−0.006	0.030
	Parasitism[b]	−0.50 ± 0.27	−1.03	0.02
Host nestlings vs. younger cuckoo	Intercept	3.33 ± 0.68	2.00	4.66
	Date	0.016 ± 0.016	−0.017	0.048
	Par. with cuckoo[c]	−0.71 ± 0.52	−1.72	0.31
	Non-par. with cuckoo[c]	−0.03 ± 0.55	−1.10	1.05
	Age	−0.19 ± 0.09	−0.37	−0.01
Host nestlings vs. older cuckoo	Intercept	4.23 ± 0.69	2.88	5.57
	Date	−0.005 ± 0.015	−0.034	0.024
	Par. with cuckoo[c]	−1.81 ± 0.44	−2.68	−0.94
	Non-par. with cuckoo[c]	−0.79 ± 0.44	−1.66	0.07
	Age	−0.20 ± 0.08	−0.36	−0.03

Estimates for years are not listed in the table (year serves only as covariable and we do not interpret it)

par. parasitized nest, *non-par.* non-parasitized nest

[a] Best model (see Table 2)

[b] Reference level: non-parasitized

[c] Reference level: non-parasitized nests with own nestlings

nest contents during incubation was also recorded (Gehringer 1979; Gärtner 1981; Schulze-Hagen 1992). Based on the mafia hypothesis (Zahavi 1979; Soler et al. 1995), the cuckoo female could check the nest contents and predate it if she found that hosts have ejected her egg. If cuckoo females were able to recognize their own eggs (Avilés et al. 2006; Cherry et al. 2007; Honza et al. 2014), they would thereby create new opportunities for successful parasitism in future as hosts frequently renest quickly after breeding failure (Cramp 1992). The predation of nests containing a cuckoo egg by the same female which laid it would be completely maladaptive in the absence of this "mafia" behaviour, because she would thereby kill her own progeny. Interestingly, the difference in survival between parasitized and non-parasitized nests almost disappears during the nestling stage (especially in GRW). This suggests that predators focusing on nests in the egg stage could be responsible for lower daily survival rate of parasitized nests during the incubation stage. These predators could be other cuckoo females which did not parasitize the particular nests. Such predation of host nests creates new opportunities for brood parasitism (Hauber 2014) without recognition of cuckoo own eggs which would be necessary according to "mafia" scenario (Zahavi 1979). The second explanation for lower nest survival of parasitized nests in the incubation stage but not later could be simply the fact that the negative effect of brood parasitism on nest predation should weaken over the time as the most conspicuous parasitized nests are gradually depredated.

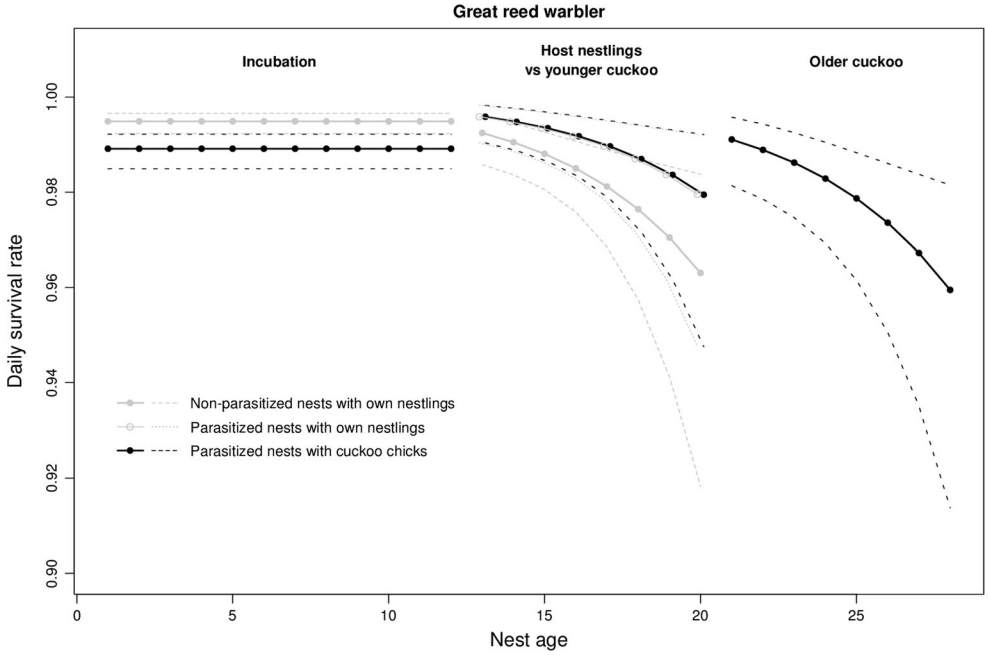

Fig. 2 Predicted daily survival rates of great reed warbler nests in relation to nest age (in days) in each nest survival analysis (incubation, host nestlings vs. younger cuckoo and host nestlings vs. older cuckoo; for more detailed description see Methods section). The similar values for parasitized nests with own nestlings and parasitized nests with cuckoo chicks are horizontally displaced to be clearly visible. Estimates were gained from the full models predicting survival of great reed warbler nests for each parasitism group on June 7 (the day, when the maximum number of great reed warbler nests in incubation, nestling and older cuckoo stage were active). The *lines with symbols* represent estimated daily survival rates of nests in particular parasitism group (Table 1) with the corresponding 95 % confidence intervals (*dashed or dotted lines*)

The probability of nest survival did not differ between nests containing cuckoo or host own nestlings during the nestling stage (up to the ninth day of age). This is in accordance with our predictions that nests with younger cuckoo chicks do not

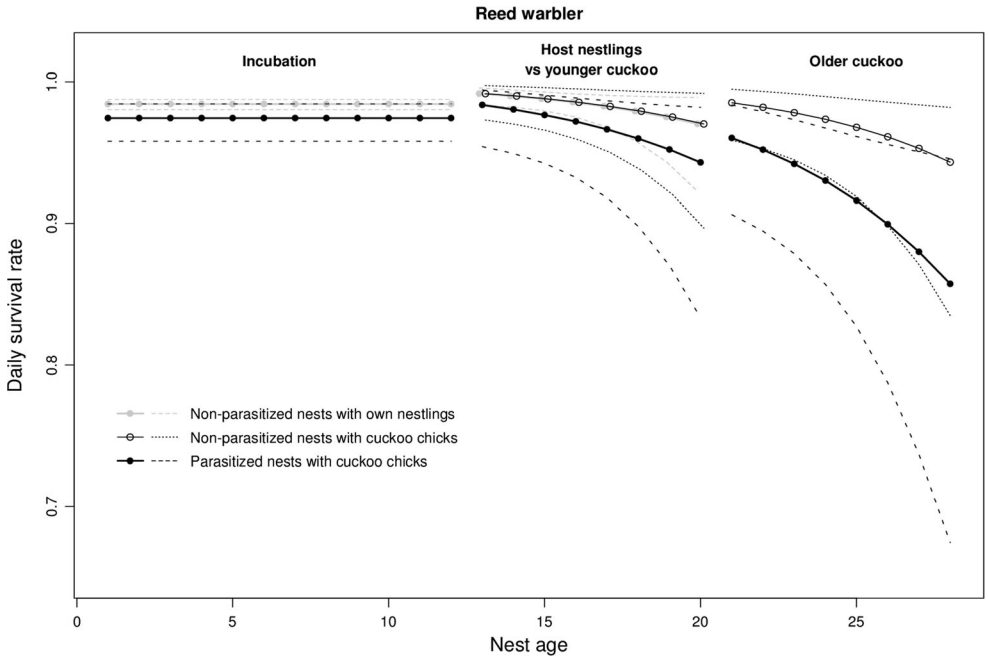

Fig. 3 Predicted daily survival rates of reed warbler nests in relation to nest age (in days) in each nest survival analysis (incubation, host nestlings vs. younger cuckoo and host nestlings vs. older cuckoo; for more detailed description see Methods section). The similar values for non-parasitized nests with own nestlings and non-parasitized nests with cuckoo chicks are horizontally displaced to be clearly visible. Estimates were gained from the full models predicting survival of reed warbler nests for each parasitism group on June 16 (the day, when the maximum number of reed warbler nests in incubation, nestling and older cuckoo stage were active). The lines with symbols represent estimated daily survival rates of nests in particular parasitism group (Table 1) with the corresponding 95 % confidence intervals (*dashed or dotted lines*)

differ from nests with host nestlings neither in appearance as both GRW and RW nests accommodate small cuckoos very well, nor in begging intensity as shown by Davies et al. (1998) and Kilner and Davies (1999) in experiments with cuckoo and RW nestlings of similar age. They found that young cuckoo chicks beg at similar rates as a full brood of reed warblers indicating the same acoustic stimuli for predators in both types of nests. However, this could be different in the GRW. As the GRW is three times bigger than the RW (Cramp 1992), we can expect that GRW nestlings beg louder than RW nestlings (Briskie et al. 1999), while the size of the cuckoo chick before the ninth day of age is similar in both host species (Kleven et al. 1999; MH and PP unpublished results). Nonetheless, also in GRW, predation of nests with brood parasites and host nestlings did not differ during the nestling stage (up to the ninth day of age).

Any predation cost of begging should instead manifest itself when the cuckoo chick grows older. Our results confirm this intuitive expectation as daily survival rate continued to decrease with age also during the older cuckoo stage in both host species (Table 3). Nonetheless, contrary to our predictions predation of older cuckoos (from the ninth to the 17th day of age) was not higher than predation of host nestlings (till ninth day of age) in the GRW. However, we found support for our prediction in the RW. Older RW cuckoos were predated more often than RW nestlings, which corresponds with our prediction that this should be a consequence of higher begging activity of cuckoos. Unfortunately, to date nobody has precisely characterized the ontogeny of begging intensity and especially the loudness of cuckoo and host nestlings across the whole nestling period despite that exuberant cuckoo solicitation likely increases their vulnerability to predators (Dearborn and Lichtenstein 2002; Haskell 2002; Davies 2011). Nonetheless, we can expect from previous studies (Kilner et al. 1999; Kilner and Davies 1999; Butchart et al. 2003), PP et al. personal field experience and unpublished data that older cuckoo chicks exhibit more intense begging behaviour at least in call rate (Kilner and Davies 1999). Butchart et al. (2003) showed that 14-day-old cuckoos beg at an approximately 2.5 times higher rate than 9-day-old RW nestlings, and furthermore, this difference seems to grow further. Moreover, except for the "normal" begging in the presence of foster parents, older cuckoos (Šicha et al. 2007) also exhibit a second type of vocalization in the absence of foster parents, consisting of distinct 'si' sounds repeated at intervals of 0.5–5 s (Lanz in Glutz von Blotzheim and Bauer 1980; Wyllie 1981; Šicha et al. 2007) which could also lure predators to the nest as well as the conspicuous wing-shaking of older cuckoos performed during parent–present begging (Grim 2008). On the other hand, in contrast to warbler nestlings which in danger only crouch down in the nest (Cramp 1992; Davies et al. 2004), cuckoo chicks are capable of specific defence behaviour. They fluff up feathers, partially spread wings, rise up, quiver in the nest and attack the enemy by pecking (Wyllie 1981). They also excrete foul-smelling liquid with a repellent effect on nest predators (Trnka et al. 2016). However, as these behaviours are mainly displayed later (after the sixth or the seventh day of age; Trnka et al. 2016), they cannot explain our results at the nestling stage truncated by the ninth day.

Our results also show that older cuckoo chicks survive considerably worse than host own nestlings only in the RW. This is not surprising as the GRW is three times larger and, more importantly, much more aggressive, capable of deterring at least some predators by contact attacks (Røskaft et al. 2002; Požgayová et al. 2009; Čapek et al. 2010), which can even result in death of the intruder (Molnár 1944; Janisch 1948; Mérő and Žuljević 2014). The spacious GRW nest can also comfortably accommodate large cuckoo chicks much better and for a longer period of time (approximately till the 18th day of age; PP et al. unpublished results) than the small RW nest, where older cuckoos have to sit on the nest rim or on the remains of the nest being quite conspicuous much earlier (approximately from the 12th day of age; PP et al. unpublished results). Although this difference in survival between older GRW and RW cuckoos is interesting, to precisely test hypotheses explaining the difference between the two host species, it will be necessary to analyse nest survival data in additional host species with different body size and variable aggressive behaviour towards intruders.

Thanks to our "experimental design"; we also tested the relationship between brood parasitism and nest predation in nests with the same contents (own nestlings in GRW and cuckoo chicks in RW, see Fig. 1). As parasitized nests are more frequently depredated than non-parasitized nests during incubation (this study), we expected the same relationship also in the nestling stage. However, this was not the case. Only in the RW, we found a weak tendency of parasitized nests with cuckoos to survive worse (estimate ± SE = −1.02 ± 0.59, CI = −2.16 – 0.12) than originally non-parasitized nests with experimentally added cuckoo chicks used as a reference group (see also Fig. 3).

In contrast to cuckoos, cowbirds (*Molothrus* spp.) are reared alongside host nestlings which favours the evolution of more intensive begging to gain more food (Gochfeld 1979; Briskie et al. 1994; Dearborn 1998; Lichtenstein 1998). This is why many studies tested for the relationship between the presence of cowbird nestlings in the nest and the probability of its depredation. Some studies found no difference in nest loss between nests with and without cowbird nestlings (Mermoz and Reboreda 1998; Burhans et al. 2002; Astie and Reboreda, 2006), while others showed better survival of non-parasitized nests (Massoni and Reboreda 1998; Ortega and Ortega 2003; Hannon et al. 2009; Stumpf et al. 2012). Finally, Hauber (2000) found that parasitized nests of song sparrows (*Melospiza melodia*) survived better than non-parasitized nests. Thus, there is no consistent conclusion whether brood parasites impose a higher predation cost of begging despite the experimental evidence that louder artificial nests are more

frequently depredated than quieter nests (e.g. Haskell 1994; Leech and Leonard 1997; McDonald et al. 2009). The experiment of Ibáñez-Álamo et al. (2012) who added great spotted cuckoo chicks into blackbird nests and showed a markedly worse survival of parasitized nests than control nests did not shed more light on this problem either. At first glance, it seems that the enhanced acoustic activity of brood parasites in the host nests considerably increases their predation (only 27 % of nests with great spotted cuckoo chicks survived in contrast to 75 % in nests with blackbirds). However, it must be pointed out that the great spotted cuckoos do not parasitize blackbird nests and may not be adapted for this "host" species. Begging of great spotted cuckoos could be tuned to particular host species and the loudness of begging calls which might be lethally dangerous in blackbird nests, could be normally harmless in fortified and better defended magpie (*Pica pica*) nests naturally parasitized by this brood parasite.

In natural host–parasite interactions, when the higher level of brood parasite's acoustic begging could probably attract predators into the vicinity of nest, the antipredation behaviour of nestlings and parents could decrease the probability that a predator will locate the nest. Consequently, the predation cost of begging may be apparent only in small and less aggressive species as in the RW (Čapek et al. 2010) than in bigger and very aggressive GRW (Požgayová et al. 2009). Nonetheless, even in species as the GRW where the predation cost of begging is undetectable in normal circumstances, it could manifest itself when the intensity of begging is extremely high, such as in times of substantial food deficiency when nestlings have to choose between abnormally loud begging luring potential predators or certain death by starvation. As this study is to our best knowledge the first one investigating the predation of cuckoo chicks in host nests, similar studies will be needed to understand the possible differences in nest predation between cuckoo and host nestlings and the real importance of the predation cost of begging in cuckoo–host system.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Bird catching, ringing and nest checking were conducted under licence (numbers 906, 1050 and 1058) and followed rules issued by the Czech Bird Ringing Centre.

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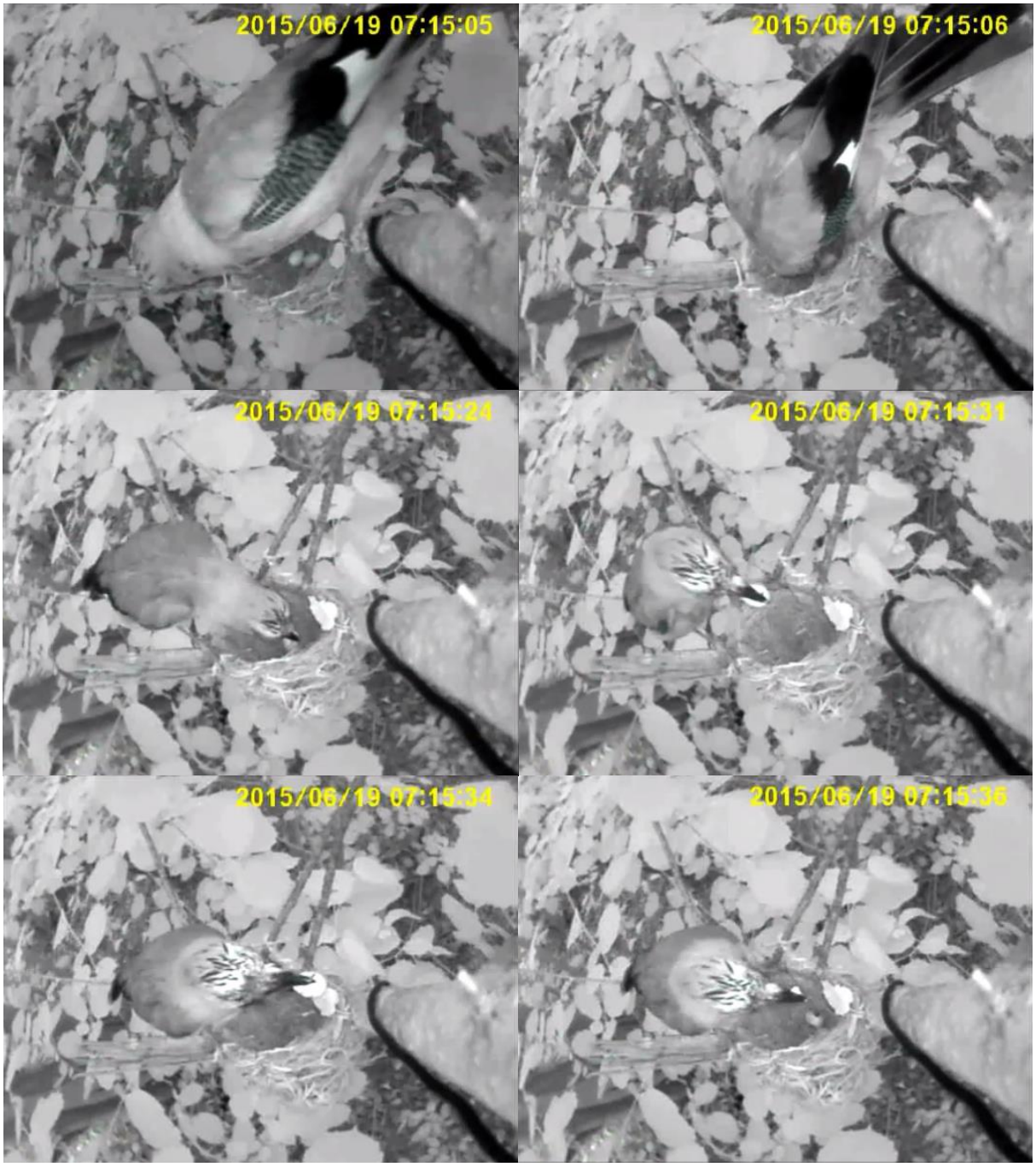
Kapitola 3

Jelínek V., Procházka P. & Honza M. (2015) Experimental enlargement of nest size does not increase risk of predation or brood parasitism in the Great Reed Warbler *Acrocephalus arundinaceus*. *Ibis* 157: 396-400.



Záznam predace umělého hnízda rákosníka velkého (*Acrocephalus arundinaceus*) sojkou obecnou (*Garrulus glandarius*).

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Short communication

Experimental enlargement of nest size does not increase risk of predation or brood parasitism in the Great Reed Warbler *Acrocephalus arundinaceus*

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We assessed whether nest size affects the probability of nest loss using dyads of large and small (large being twice the size of small) inactive Great Reed Warbler *Acrocephalus arundinaceus* nests placed at similar sites in Great Reed Warbler territories. Large nests were not predated significantly more frequently than small nests. Experimentally enlarged active Great Reed Warbler nests suffered non-significantly higher predation compared with non-manipulated control nests. Our experiments did not support the nest-size hypothesis and suggested that nest size does not appear to be a factor affecting the risk of nest predation in this species. The probability of brood parasitism by the Common Cuckoo *Cuculus canorus* was also unaffected by experimental nest enlargement, supporting the commonly accepted hypothesis that the Common Cuckoo searches for suitable host nests by host activity during nest building rather than nest size.

Keywords: Common Cuckoo, nest survival, predation.

Nest predation is the most frequent cause of nest loss (Ricklefs 1969, Best & Stauffer 1980, Lima 1987, Martin 1995) and one of the fundamental forces shaping the life histories of birds (Fontaine & Martin 2006, Lima 2009). As such, it is important to assess which features of avian reproduction are responsible for the discovery of nests by predators and for the loss of nest contents by subsequent predation, particularly as there should be selection to minimize predation through factors such as choice of nest-site. Although parents have some behavioural options that allow them to lower the probability of nest detection (e.g. inconspicuousness near the nest or aggression towards the predator), once the nest is discovered by a predator, the chances of forestalling nest loss are often limited (Pierce & Pobprasert 2013). Hence, choosing a safe nest-site is crucial for reproductive success (Martin 1998, Weidinger 2002, 2004).

Another variable that may affect the probability of nest survival is nest size. The nest-size hypothesis proposes a positive relationship between nest size and the probability of predation, larger nests being more conspicuous and thus subject to higher predation (Snow 1978). As support for this hypothesis is scarce in observational studies (Antonov 2004, but see Møller 1990, Lent 1992, Palomino *et al.* 1998), and equivocal in experimental studies (Slagsvold 1989, Møller 1990, Weidinger 2004, Biancucci & Martin 2010), it seems reasonable to assume that the effect of nest size may often be masked by parental activity or other factors. Experimental investigation using controlled design of artificial nests enables evaluation of the nest-size hypothesis without the confounding effect of parental activity.

We tested experimentally the nest-size hypothesis using dyads of real but inactive Great Reed Warbler *Acrocephalus arundinaceus* nests of different sizes (collected in previous years) placed at similar sites near active Great Reed Warbler nests. We predicted that larger experimental nests would suffer greater predation than smaller nests. We also experimentally enlarged a sample of active Great Reed Warbler nests to assess the effect of nest-size manipulation on nest survival in the presence of parents. Finally, we assessed whether nest-size manipulation affected nest vulnerability to brood parasitism by the Common Cuckoo *Cuculus canorus*.

METHODS

This study was conducted between 20 April and 20 July in 2011 and 2012 in two adjacent fishpond areas between Hodonín (48°51′N, 17°07′E) and Mutěnice (48°54′N, 17°02′E) in South Moravia, Czech Republic. The littoral vegetation was dominated by Common Reed *Phragmites australis*, with a smaller proportion of Narrow-leaved Cattail *Typha angustifolia*. The majority of reed beds were belt-shaped and of uniform width (up to 20 m wide), although width differed between fishpond dykes. The Great Reed Warbler population at this site

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numbered between 80 and 100 pairs and all individuals were marked with a unique combination of a standard aluminium ring and up to three coloured plastic rings. We regularly mapped territories upon male arrival and checked them every 2 days to assess male mating status (Bensch 1996). Later in the season (June–July), territories were checked less frequently. If we recorded the switch between long and short song, signalling the presence of a female in the territory (Catchpole 1983, Hasselquist & Bensch 1991), we immediately tried to find an unfinished nest. Consequently, all nests used in this study were found during the building stage or at the beginning of egg-laying and were checked daily until clutch completion to reveal possible Cuckoo parasitism. Thereafter, the nests were checked less often (typically every 4 days). Each nest was tagged with a small piece of coloured tape and its GPS (Garmin OREGON 300®) location recorded.

Nest measurement and nest-site characteristics

Nest and nest-site characteristics were recorded immediately after building was completed in enlarged nests (prior to enlarging) and at the same time or prior to laying of the fourth egg in control nests. The following variables were recorded: water depth under the nest, distance to open water, distance to the shore, reed height above the water's surface, height of upper nest rim above water or ground level, height of vegetation above nest, reed density (estimated as sparse, intermediate or dense), nest height (obtained as the mean of two measurements), and cuckoo nest view, scored following the protocol of Øien *et al.* (1996). All dimensions were recorded by the same person (V.J.).

Nest predation experiment

For the nest predation experiment, we used 50 dyads of small and large nests (30 in 2011 and 20 in 2012) composed of Great Reed Warbler nests collected in previous years. The small nests were 12 ± 1 cm high (first quartile of nest heights from 373 nests measured between 2008 and 2010) and each large nest was twice the size of its smaller counterpart (24 ± 1 cm). The large nests were constructed from up to four old nests (one nest being placed on top of the other) tied together with black lashing wire (Supporting Information Appendix S1). We ensured that both the small nests and the uppermost of the large nests had intact nest cups. As each dyad comprised nests of similar width built from similar materials, nest height served as an accurate proxy of nest size. The experimental nests were baited with three European Greenfinch *Chloris chloris* or Common Linnet *Linaria cannabina* eggs filled with plasticine and tied to the nest cup with thread. The experimental nests of each dyad were placed 10 m on either side of an active Great Reed Warbler nest (usually parallel to the fishpond shore) at sites with the same habitat characteristics as the active focal nest (see nest measurement and recorded variables). Nests were fastened to reed stems using jute string (Appendix S1) at the time when the third egg was laid in the focal nest. The artificial nest dyads were placed in the field during the peak breeding season, from 11 May to 17 June, in both years. The experimental nests were checked every 6th day over the total exposure period of 30 days, corresponding to the approximate length of a successful nesting attempt (from clutch initiation to fledging). A nest was classified as predated if one or more eggs were damaged or missing, whereupon the nest was immediately photographed and removed. Whenever we found marks on the eggshell or plasticine, we determined the predator based on Ludwig *et al.* (2012). We classified egg predators as mammalian or avian and as small or large (see Supporting Information Appendix S2 for details on predator classification, including a species list of potential predators).

Experimental enlargement

In combination with another study examining the role of nest size as a post-mating signal between partners, we enlarged a total of 33 active Great Reed Warbler nests in 2011 (n = 18) and 2012 (n = 15). Active nests were enlarged during the measurement procedure by attaching old Great Reed Warbler nests collected in previous years below the active nest. The old nests were carefully selected to be as similar as possible in appearance (size, shape and type of nest material) to the experimental nests. The nests were tied to the reed stems supporting the experimental nest using jute string (Appendix S1). Sometimes we tied new supporting reed stems to the nest and cut some of the supporting reed stems *c.* 50 cm above the nest's rim in order to increase the stability of the enlarged nest. Mean nest height ± 1 s.d. before enlargement was 12.4 ± 1.6 cm (range 9.7–16.5 cm) and mean nest height ± 1 s.d. of the control nests was 12.0 ± 2.5 cm (range 8.9–16.8 cm). Control and enlarged nests did not differ in nest-site characteristics. All comparisons were conducted using Wilcoxon signed-rank tests as the data frequently did not comply with normality (all P-values >0.31). Nest height after experimental enlargement was similar to that of the artificial large nests used for the nest predation experiment, i.e. 24.0 ± 1 cm (see above).

Manipulation took place during the pause between the building and egg-laying phases, thereby preventing nest desertion as a direct result of the enlargement procedure. The nests were then checked each day during the egg-laying period; there was no difference in predation of the experimental and control nests immediately after manipulation. For control nests, we chose nests

located in territories close to the experimental nests, and at the same time in order to avoid potential problems with different predators being present or other confounding variables.

Active nests were regarded as successful when nestlings survived to their 9th day, and depredated if part or the whole nest contents disappeared during the incubation or nestling phases, thus causing termination of the nesting attempt. When we found a Cuckoo egg in the nest, we classified the nest as parasitized.

Statistical analysis

Due to the paired design of the nest predation experiment, we used McNemar's Chi-square test with continuity correction to determine whether large experimental nests were predated more frequently than small nests. Fisher's Exact test was used to assess whether the real enlarged nests were predated more frequently than the control nests and the Chi-square test for comparison of parasitized and non-parasitized nests.

RESULTS

Artificial nests

To examine predation, we excluded one of the 50 experimental dyads, as the large nest had been parasitized by a Cuckoo. In 17 cases both nests in the dyad were predated and in 15 cases both nests remained intact for the whole 30-day exposure. Of the 17 remaining dyads, only the small nests were predated in six cases and only the large nests in 11 cases. Predation did not differ significantly between large and small nests in the dyads (McNemar's $\chi^2 = 0.941$, $P = 0.332$, odds ratio = 1.83, confidence interval (CI) = 0.68–4.96). We were able to assign the type of nest predator in 48 of 51 predation events. In 12 cases we identified mammalian predators (two nests by large and 10 by small mammalian predators) and in 36 cases avian predators (22 nests by large and 14 by small avian predators). We were unable to assign predators to three small nests as there were no beak or teeth marks on the eggs; however, we believe that these nests were predated by birds. Birds predated 23 of 28 large nests and 13 of 20 small nests.

Enlargement of real nests

We enlarged a total of 33 nests (18 in 2011 and 15 in 2012), nine of which were deserted as a consequence of Cuckoo parasitism and one probably as a consequence of the enlargement procedure. Two of the 30 control nests were deserted due to brood parasitism by the Cuckoo, leaving 23 enlarged nests and 28 control nests for predation analysis. Of these, seven enlarged and two control nests were predated. Fisher's Exact test indicated that the enlarged nests were depredated marginally non-significantly more frequently than control nests ($P = 0.061$, odds ratio = 5.69, CI = 0.90–60.61).

Brood parasitism

In three cases, the experimentally enlarged nests were parasitized by Cuckoos before enlargement; hence, these nests were excluded from the analysis. Of the 30 remaining enlarged nests and 30 real active nests (considered as controls), 14 enlarged and 13 control nests were parasitized over subsequent days. The probability of parasitism did not differ between these two groups ($\chi^2 = 0.067$, $P = 0.80$, odds ratio = 1.14, CI = 0.37–3.57).

DISCUSSION

Experimental studies investigating the effect of nest size on nest survival usually use differently sized real nests installed at the nest-site of real birds after termination of their breeding attempt. Weidinger (2004) exchanged nests of three species with different-sized nests and found that, although the predation rates differed between species (combined effect of site and size), only the effect of nest-site remained significant after the exchange. In contrast, a similar study of Biancucci and Martin (2010) showed a positive relationship between the size of nest and predation. A similar result was also found by Møller (1990) for Common Blackbird *Turdus merula* nests.

Adopting the same experimental procedure in reed beds could be problematic, as rapid vegetation growth during the breeding season could cause a pronounced difference between the original and experimental nest-sites, despite using the same places. The homogeneous structure of reed beds, however, allowed us to adopt a slightly different experimental approach. We placed dyads of differently sized old Great Reed Warbler nests in similar sites as focal active nests, which served as natural models for our experimental nest-sites. Thus, we were able to investigate nest predation at the same time as real focal nests were active without the confounding effect of parental behaviour.

We observed no significant difference in depredation between large and small nests, indicating that nest size does not influence the risk of nest loss. Our findings do not correspond to those of López-Iborra *et al.* (2004), who placed old nests of two sizes (Great Reed Warbler and the smaller Eurasian Reed Warbler *Acrocephalus scirpaceus* nests), baited with quail *Coturnix* and plasticine artificial eggs, in linear transects along the edge of reed beds and found that Great Reed Warbler nests were predated significantly earlier. Nonetheless, results of that study should be interpreted with care because almost all

(97%) the experimental nests were depredated during the short 14-day exposure. The predation rate in our experimental nests, in contrast, was much lower, with just 52% of nests (51 of 98) being predated during 30-day exposure. This may have been due to differing densities of some nest predator groups between the two study sites. At the Spanish site of López-Iborra *et al.* (2004), around 30% of the nests were predated by small rodents and almost 50% by large predators. Our nests, in contrast, were predated by small rodents in 20% of cases and damaged or torn by large predators in only 12% of cases.

The predation rate of real Great Reed Warbler nests was lower than that of the inactive artificial nests, reaching around 17% (n = 640; deserted nests excluded; P. Procházka, V. Jelínek, M. Honza unpubl. data). We recorded the same predation rate (17%) when we enlarged real active Great Reed Warbler nests. Despite the potential confounding effect of parental activity, enlarged nests were predated more frequently than the controls, although the result fell just short of statistical significance at $P < 0.05$.

Since Great Reed Warbler nest size varies greatly (Fig. 1), we used the upper limit of real nest size in our experiments (3% of 602 nests measured during 2008–2012 were the same as or larger than our large experimental nests) to magnify the potential effect of nest size on predation. This enabled us to reveal any relationship, even if the effect was relatively small or undetectable due to low nest-size variability in the real nest observational data. Despite this, results of both the artificial nest experiment and the real nest enlargement experiment did not support the nest-size hypothesis, although the result of the latter was close to significant.

One possible explanation for these results could be that the Great Reed Warbler is a very aggressive species (Trnka & Prokop 2012, Požgayová *et al.* 2013), quite capable of effectively defending its nest. Hence, although a range of predators may have been attracted to the larger nests, only large predators, such as the Western Marsh Harrier *Circus aeruginosus* or American Mink *Mustela vison*, succeeded in predating the nest. Validation of this hypothesis will be difficult (or impossible), however, without precise identification of predators through photographic or video recording.

An alternative explanation of our result is the reporting of a false positive effect of nest size due to the presence of a Type I error. Although the first possibility cannot be completely ruled out, the second seems more plausible, especially when only one (Antonov 2004) of nine previous studies (Møller 1990, Lent 1992, Hatchwell *et al.* 1996, Palomino *et al.* 1998, Wilson & Gende 2000, Herranz *et al.* 2004, Suárez *et al.* 2005, Humphreys *et al.* 2007) has found support for the nest-size hypothesis in real active nests at the within-species level.

Nonetheless, if our determination of predators is correct and birds were responsible for 75% of predation events in all nests and 80% in the large nests, the effect of nest size (expressed mainly as height) on predation could be reduced, as birds (especially large ones) locate nests from above. On the other hand, although mammals probably have a better view on the nest during searching for prey, they mostly locate their prey at night using olfactory rather than visual stimuli. This could also reduce the impact of nest size on predation.

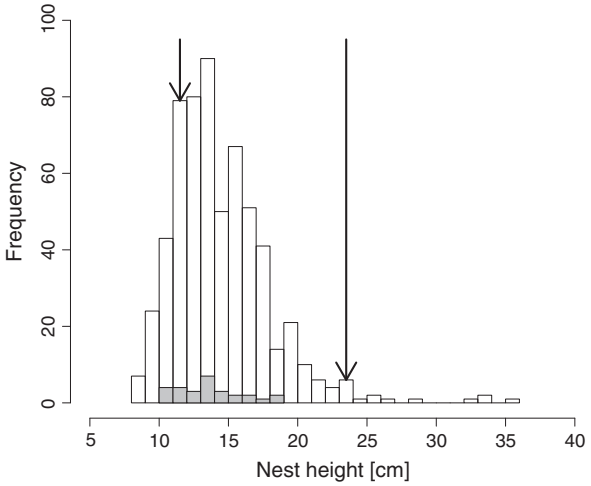

Figure 1. Histogram of nest heights used as a proxy of nest size for all Great Reed Warbler nests measured during the 2008–2012 breeding seasons (n = 602). Arrows show the nest height of enlarged and large artificial nests (long arrow) and small artificial nests (short arrow) used in the predation experiments. The grey histogram shows the nest heights of control Great Reed Warbler nests (n = 28).

Finally, it must be pointed out that, in contrast to other species, nest predation is not the major cause of nest loss in our Great Reed Warbler population. Cuckoos, for example, represent at least as great a threat to Great Reed Warbler nests, with more nests failing due to brood parasitism (approximately 20%; P. Procházka, V. Jelínek, M. Honza unpubl. data) than to predation (17%). Nest size probably does not affect the probability of brood parasitism either, as neither real large nonmanipulated (Moskát & Honza 2000, Jelínek *et al.* 2014) nor our real enlarged nests were parasitized preferentially by the Cuckoo. Thus, our results suggest that neither brood parasitism nor predation offers a sufficiently strong selection pressure to force Great Reed Warbler females to build smaller nests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Nest size variability.

Appendix S2. Predators of artificial nests

Nest size variability

- (2-3) – Size and material variability of Great Reed Warbler (*Acrocephalus arundinaceus*) nests

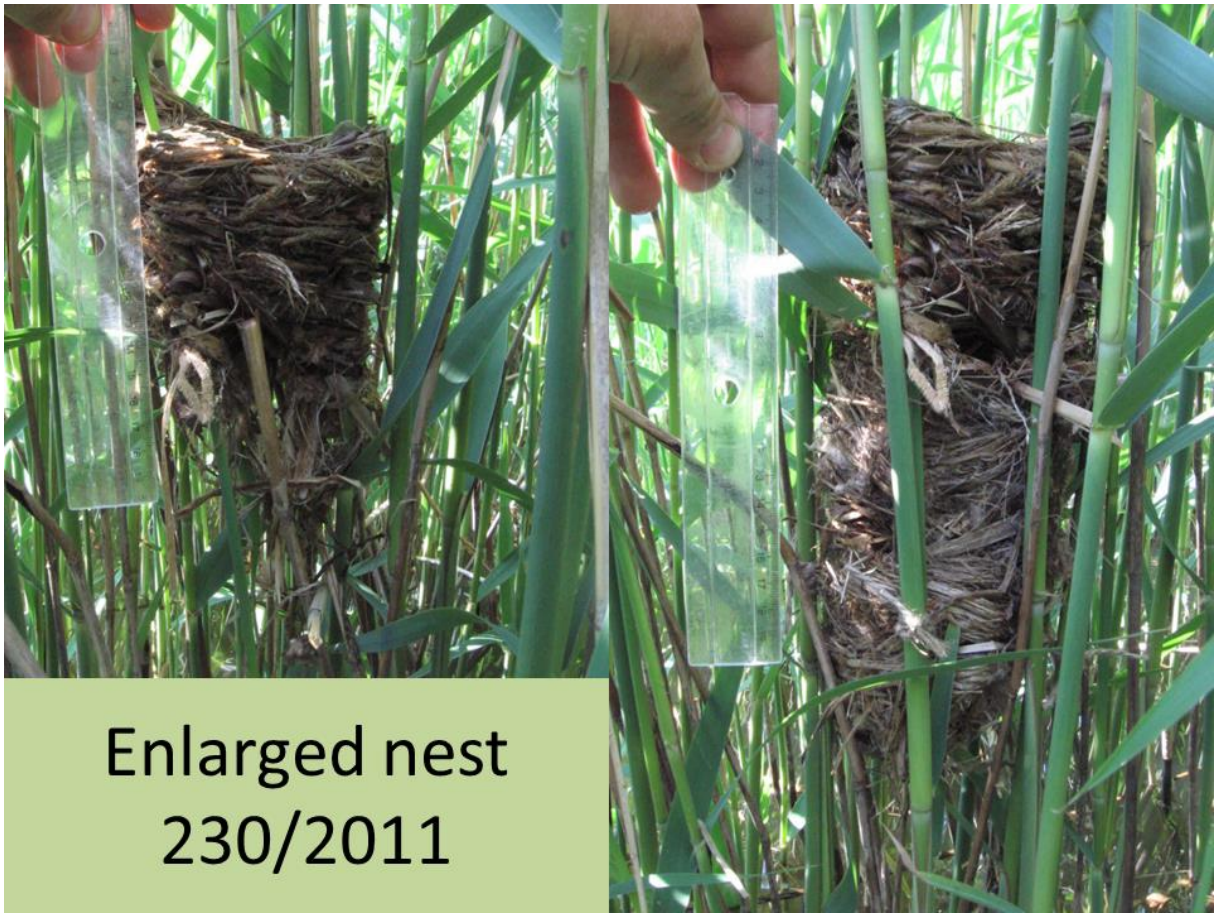
Enlargement experiment

- (5-9) – Some experimental nest before and after enlargement.
- (10-14) – Comparison of sizes of enlarged nests and large unmanipulated nests
- (15-16) – Photos of some control nests

Enlarged nest 217/2011

Enlarged nest 514/2012


Enlarged nest
439/2012


Enlarged nest
230/2011


Enlarged nest
520/2012


Natural nest 914/2012
Enlarged nest 514/2012

Natural nest 229/2009 Enlarged nest 103/2011

Natural nest 204/2013 Enlarged nest 424/2012

Natural nest 123/2008 Enlarged nest 524/2012

Natural nest 135/2013 Enlarged nest 901/2012

Control nests:

102/2011 512/2011 214/2011

Control nests:

915/2012 536/2012 318/2012

Experiment with artificial nests

- (18-19) – Pairs of small and artificial nests
- (20) – Detailed photos of two large nests
- (21-22) – Comparison of large nests

- Please note, that these nests were already used in field. They were depredeted or exposed to weather conditions for 30 days, transported and stored for one or two years in boxes. Thus their condition need not neccessarily be the same as when they were used.

Small and large artificial nest (1)

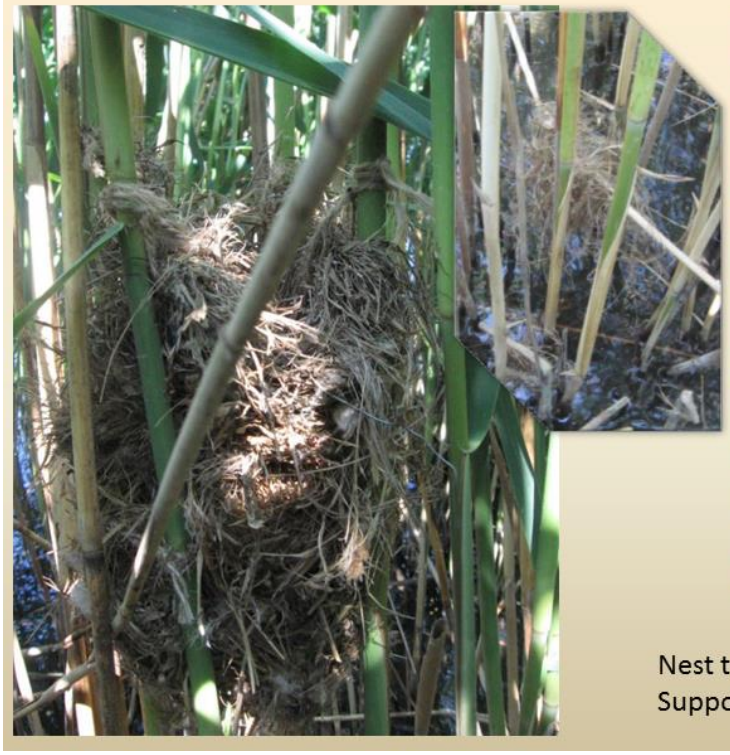
Small and large artificial nest (2)

Details of large artificial nests

Predators of artificial nests

- Photos of traces of predators on nests and their marks on eggs.
- Predators were classified as mammals and birds (small or large).
- The more detailed description of features by which nests were classified are written bellow pictures.

Large mammal



Nest teared apart without eggs.
Supposed predators: mink.

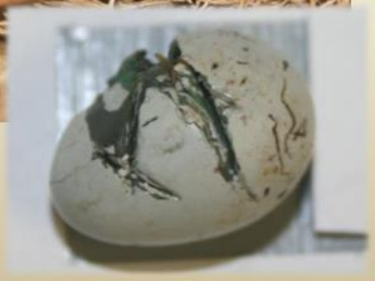
Small mammal

Nest untouched.
Often large pieces of eggshell removed.
Plasticine with many small scratches (sometimes clear marks of incisors).
Supposed predators: small rodents.

Large bird

Nest demaged.
Eggs with long straight and slender cuts. Some eggs often pull out.
Another eggs in following picture.
Supposed predators: Marsh Harrier.

Large bird



Supposed predators:
Little Bittern, Common Cuckoo or Jay

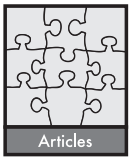
Small bird

Nest untouched.
Small cracks, scraches and especially pecks (the most typically of triangular shape) in eggshells.

Kapitola 4

Jelínek V., Požgayová M., Honza M. & Procházka P. (2016) Nest as an extended phenotype signal of female quality in the great reed warbler. *J. Avian Biol.* 47: 428-437.

Příklady různě velkých sous, které rákosníci velcí (*Acrocephalus arundinaceus*) přinášení svým mláďatům.



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Nest as an extended phenotype signal of female quality in the great reed warbler

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Extended phenotypes with signalling function are mostly restricted to animal taxa that use construction behaviour during courtship displays. However, they can be used also as post-mating signals of mate quality, allowing individuals to obtain reliable information about their partners. Nest size may have such a signalling function and a lot of indirect evidence supports this view. However, direct evidence based on an experimental approach is still widely missing. Here we test the role of nest size in post-mating signalling of mate quality in the great reed warbler *Acrocephalus arundinaceus*, a passerine with female-restricted nest-building behaviour. Based on observational data, clutch size, nestling weight, brood size and fledglings' propensity to return to their natal site positively correlated with nest size. Moreover, we experimentally enlarged great reed warbler nests to investigate whether this manipulation affects male investment in feeding. We found that males fed their nestlings significantly more intensively on enlarged nests than those on control nests. This suggests that nest size in this species serves as a signal of female quality or willingness to invest in reproduction and that it pays males to enhance their feeding effort according to this signal. Thus, we provide convincing evidence that animal communication takes place through the extended phenotypes and that post-mating signalling of quality is not restricted only to males, but may function equally well in females.

Animal signals are used to increase the fitness of one individual by affecting the behaviour of others which simultaneously try to use the same signals to increase their own fitness (Endler 2000). Signals frequently take a form of acoustic (e.g. singing, warning calls), visual (feather or skin coloration) or olfactory (scent marks) stimuli. Extended phenotypes can serve as signals as well. These non-bodily signals are used by a variety of taxa from Protista to mammals (Schaedelin and Taborsky 2009), however, they are the most elaborate and studied in species exhibiting construction behaviour, like fish or birds. Typical examples of extended phenotypes with exclusive signalling function are bowers of bowerbirds or courtship areas of cichlids (Schaedelin and Taborsky 2009) which serve as secondary sexual traits to attract females (Borgia 1985, McKaye et al. 1990, Hansell 2000, Kellogg et al. 2000). Besides, extended phenotypes with primarily non-signalling function can secondarily serve as signals too. The blue-green egg colouration in some bird species (Moreno and Osorno 2003) or avian nests are two notable examples (Moreno 2012).

The main purpose of avian nests is to protect offspring (Hansell 2000) or reduce energy demands associated with incubation (Walsberg and King 1978, Hansell 2000). However, in species, like weavers (family Ploceidae), penduline tit *Remiz pendulinus* or winter wren *Troglodytes troglodytes*, they are built exclusively by males and are used by females as a clue during mate choice (Persson and Öhrström 1989, Evans and Burn 1996). In these cases, nest building is essential for male fitness as a secondary sexual trait and can be the male's only way how to participate in reproduction, except for siring the offspring (Persson and Öhrström 1989). On the other hand, the nest, and especially its size, may also serve as a signal of quality after mating as posited by the sexual display hypothesis (Moreno et al. 1994, Soler et al. 1998a).

The idea of post-mating signalling of quality is based on the differential allocation hypothesis. According to this hypothesis, mates of more attractive individuals are willing to contribute more to parental investment compared to mates of less attractive individuals (Burley 1986). However, these less attractive individuals can compensate for lower participation of their mates or even stimulate them to increase their parental investment (Soler et al. 1998b).

As the visual attractiveness expressed by secondary sexual traits serves as a clue in mate choice, the willingness to invest more in reproduction should be advertised by other signals. The nest size may be one of them. Its role in post-mating signalling of mate quality was best explored in magpies *Pica pica*, (De Neve and Soler 2002, De Neve et al. 2004), where both partners participate in nest building (Birkhead 1991).

Soler et al. (2001) showed that experimental manipulation of nest size significantly influenced magpie reproductive behaviour. In reduced nests females laid fewer eggs and started incubation earlier than in control or enlarged nests which caused larger hatching asynchrony and subsequent greater differences in nestling size. Similarly, in blue tits *Cyanistes caeruleus*, where the nest is built almost exclusively by the female, males with reduced nests were shier than those with control or enlarged nests while their feeding behaviour did not change (Tomás et al. 2013). Unfortunately, the methodology the authors used to characterize the risk-taking behaviour does not allow determination of the particular behavioural features affected by nest size manipulation. Other studies showed that nest size correlated with various traits reflecting quality of adult birds (Palomino et al. 1998 and Soler et al. 1998b – laying date and clutch size, Avilés et al. 2009 – feeding of nestlings, see Moreno 2012 for other examples), however, the experimental approach is essential to distinguish whether the nest size serves as a signal or is only a correlate of mate quality.

Here we tested the signalling function of nest size in the great reed warbler *Acrocephalus arundinaceus*. In this species the nest is built exclusively by females, males participate only in nest guarding, nest defence, and feeding of nestlings (Cramp 1992). Moreover, frequent polygyny in this species (Bensch 1996, Trnka et al. 2012) indicates that males are the less choosy sex. Therefore, it should be adaptive to evaluate female quality after mating by a cue or signal such as nest size. This would be beneficial especially to polygynous males which care for two or more simultaneous broods and thus may allocate their paternal effort according to this signal.

Firstly, we tested on an extensive observational dataset whether larger great reed warbler nests could be of 'better quality' in terms of reproductive traits. We hypothesized that more eggs will be laid and more nestlings will be nurtured in larger nests, nestlings in larger nests will be heavier and will survive better, as manifested in their higher return rate in subsequent years. Secondly, we explored whether the nest size influences male (or female) parental effort during nestling provisioning using the correlational data as well. As the results of these analyses were equivocal and positive correlation between nest size and reproductive traits or feeding effort need not necessarily reveal the signalling function of nest size (as in Avilés et al. 2009), we subsequently performed a manipulation experiment to test whether enlargement of great reed warbler nests affects male feeding effort and nestling weight.

Methods

The study was conducted in two adjacent fishpond areas between Hodonín (48°51′N, 17°07′E) and Mutěnice (48°54′N, 17°02′E), South Moravia, Czech Republic, from 20 April to 20 July 2008–2012. The studied great reed warbler population numbered 80–100 pairs and was heavily parasitized by the common cuckoo *Cuculus canorus*, up to 50% of nests, (Jelínek et al. 2014). All individuals were marked by a unique combination of a standard aluminium ring and up to three plastic colour rings. We mapped male territories at the beginning of the season and checked them every two days to correctly assess male mating status (Bensch 1996). If we recognized a switch between long and short song, signalling the presence of a female (Catchpole 1983, Hasselquist and Bensch 1991), we tried to find a nest still under construction, which was essential for the experimental part of the study (see below).

We found almost all nests each year and based on resightings of the unique colour ring combinations at nests during checks, nest defence experiments or from video recordings we also assigned both parents to 94% of nests (n = 643). Nests found during the building stage or at the beginning of egg-laying were checked daily until clutch completion. Thereafter, the nests were checked less often (typically every four days). Each nest was tagged by a small piece of a colour tape and its GPS location was recorded using a GARMIN OREGON 300 device. Eggs were numbered by a felt-tip pen according to their laying order to reveal missing eggs.

Nest dimensions and other recorded variables

We measured dimensions of great reed warbler nests during the egg-laying period or incubation. Some nests were found later with large nestlings or were damaged by predators or due to weather conditions before the measurements could be taken (6.8% of all 643 nests built by 329 individual females). Nest volume (V) was calculated as a half of an ellipsoid according to the formula: $V = 4/3(\pi \times a^2 \times b \times 1/2)$ where *a* is the radius of the nest and *b* height of the nest (Møller 1982). Both dimensions were obtained as the mean of two measurements of nest width and height. The underside of the nest usually terminated in loose tags of nesting material. As these contributed to the nest silhouette, nest height was measured from the nest rim to the end of these tags. All measurements were taken by one person (VJ).

Further, we recorded the following variables: laying date of the first egg (1 May = day 1), number of eggs laid, identity of breeding pairs and which fledglings returned in subsequent years. Additionally, we classified nests in terms of brood parasitism, social status and order during the season. We considered the nests as parasitized when they contained a cuckoo egg or chick. Nests with known and uninterrupted egg-laying sequences or those found later but with clutches of four or five eggs were classified as non-parasitized. All other nests were not considered in our analyses, except for the analysis of philopatry. When only one nest associated with a particular male was active, we classified it as monogamous. When more nests associated with a single male were active simultaneously, we classified them according to their order as primary, secondary or tertiary. Finally, nests built by the same female during one particular season were classified as first and first replacement.

Video-recordings and their analyses

To test the sexual display hypothesis, we filmed the nests when the nestlings were 7–9 d old (1 = day of hatching) between 8:30 and 16:00 h CET using camcorders JVC EVERIO GZ-MG730 and GZ-MG20E. The camcorders were placed 2–5 m from the nests and levelled with the upper nest rim. We recorded the overall amount of prey

delivered by each parent during three hours after habituation (hereafter referred to as male or female feeding effort). We used three criteria of habituation. We used 30 min as a habituation time (86% of 50 recordings analysed for this study). When the second parent did not come within the first 30 min of the recording, we started the analysis after its first arrival (8%). In the remaining three nests (6%) we had doubts about the successful habituation even though the second parent came and fed the nestlings. In these cases, we started the analysis 30 min after we were convinced that both birds lost the fear of the camera (mean habituation time for the third group ± SD = 113 ± 63 min). The females sometimes brooded nestlings, which reduced the time they could devote to food provisioning. Thus, we added the time each female spent brooding to the 3-h period after habituation. In one extreme case, the female brooded her nestlings for 67 min during the 3-h interval after the habituation. Thus, the analyzed time of recording was 3 h for the male and 4 h and 7 min for the female.

Prey size was scored relatively to bill size using a photographic scale and the feeding effort was computed as a sum of sizes of all prey items brought by one parent during the three hours of feeding. All video-recordings were analyzed by one person (VJ).

Feeding in non-manipulated nests

In 2009, we filmed 19 first (not replacement) monogamous nests for the analysis of the relationship between nest size and amount of prey delivered to nestlings by parents in natural non-manipulated conditions. Of these, we excluded one nest because the length of brooding by the female did not allow us to analyze 3 h of nestling provisioning.

Experimental enlargement of nests

The enlargement experiment was performed during breeding seasons 2011 and 2012 by attaching old great reed warbler nests collected in previous years below active nests (Fig. 1). We selected old nests that were most similar in appearance (size, shape and type of nest material) to the experimental ones. These old nests were tied to reed stems supporting the active nests by a jute string because it is a natural material of the same appearance as the nesting material used by great reed warblers (Fig. 1, see Supplementary material Appendix 1, for additional photos of nests before and after enlargement). The construction of a great reed warbler nest lasts on average 3–4 d followed by a 1- or 2-d pause before the female starts to lay eggs (Cramp 1992, Procházka and Honza unpubl.). Thus, we enlarged the nests during the pause between the building and egg-laying. The focal nests were measured prior to the enlargement. As controls, we chose nests located near the experimental ones, with similar timing to minimize potential bias caused by different food availability or quality in time and space.

We enlarged a total of 33 nests (18 in 2011 and 15 in 2012), 9 of which were deserted as a consequence of cuckoo parasitism, 1 probably as a consequence of the enlargement procedure, 7 depredated before the feeding could be filmed. In addition, one recording was too short for analyses due to protracted habituation and in one nest only the female fed the nestlings. Thus, we could use only 14 enlarged nests for the analyses (7 in both years). Of 30 control nests, 2 were deserted as a consequence of cuckoo parasitism and 2 were depredated. Of the remaining 26 nests, we filmed feeding behaviour of parents only in those 17 nests which had similar timing as the experimental nests and were located in the same or neighbouring fishponds. Of these nests we excluded one nest where nestlings were fed only by one parent and one recording which was too short for analyses due to protracted habituation. Therefore we included only the data from 15 control nests into the analyses (8 in 2011 and 7 in 2012).

Mean nest volume ± SD before enlargement was 0.725 ± 0.118 dm^3 (range 0.536–0.95 dm^3, n = 14) while mean volume of the control nests was 0.667 ± 0.095 dm^3 (range 0.489–0.793 dm^3, n = 15, Fig. 2). The nest volume of control nests and original volume of enlarged nests did not differ significantly (as data did not comply with normality, we used Wilcoxon rank-sum test: W = 136, p = 0.19). The height of the nests after enlargement was 24.0 ± 1 cm (double the first quartile of nest heights from 373 nests measured in 2008–2010). The mean volume ± SD of the enlarged

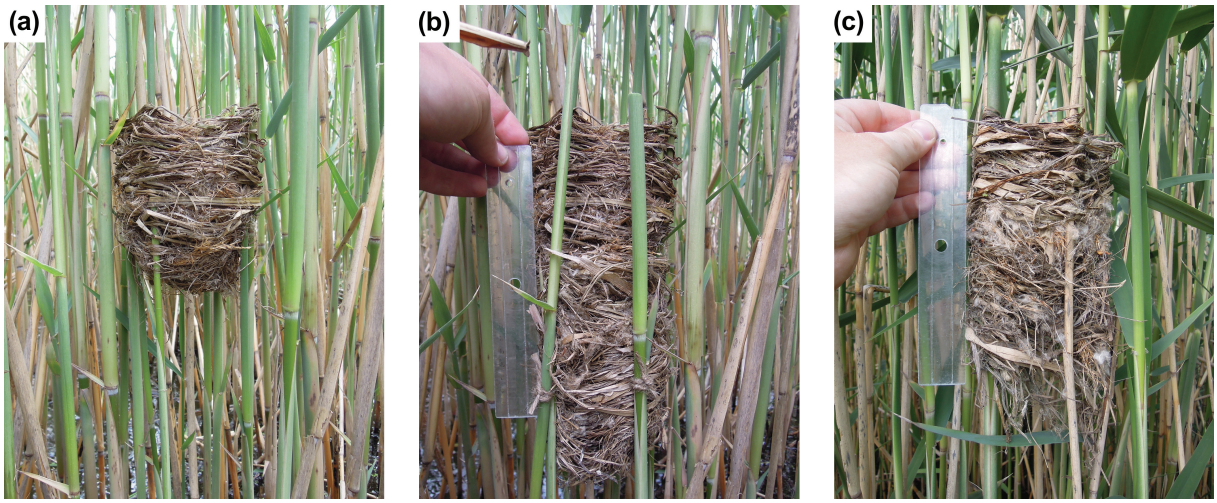

Figure 1. An example of a great reed warbler nest before (a) and after enlargement (b) and a comparison with a large natural nest (c).

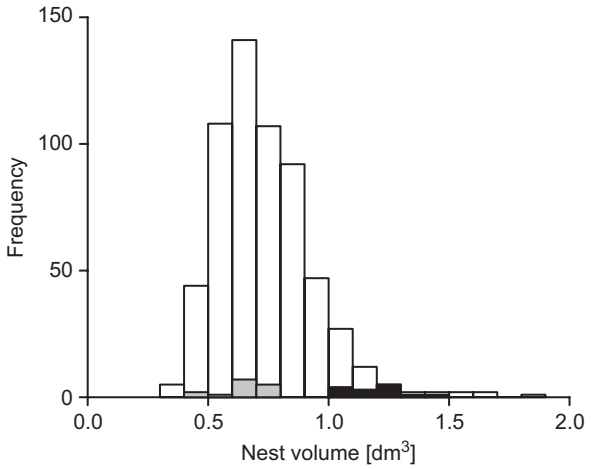

Figure 2. Histogram of volumes of all measured great reed warbler nests in breeding seasons 2008–2012 (white columns, n = 599), control nests (grey columns, n = 15) and enlarged nests (black columns, n = 14).

nests was 1.198 ± 0.111 dm^3 (range = 1.056–1.411 dm^3). Thus, the difference between the volume of experimental nests before and after enlargement was 0.473 dm^3 which is eight times more than the difference between the control nests and the experimental nests before enlargement (corresponding to a mean difference of 9.6 cm in nest height between nests before and after enlargement).

Statistical analyses

Relationship between nest size and reproductive traits

To test the relationship between nest size and clutch size, brood size and fledgling return rate, we used data from all study years (2008–2012). When multiple nests were built by the same female, we randomly selected one of them to avoid pseudoreplications. Enlarged nests were not used in these analyses. Sample sizes differ for each analysis because cuckoo predation significantly reduced the number of eggs and nestlings in parasitized nests. Thus, the subsets for testing the relationship between nest size and clutch size or brood size comprised all non-parasitized (n = 216) and successful non-parasitized (n = 171) nests, respectively. As the last day when we checked the nest contents was mostly the day when we ringed nestlings (at the age of 6–9 d) we defined brood size as a number of nestlings in the nest during this check. For these two analyses we used correlation tests based on the Spearman's rank correlation coefficient.

To test the relationship between nestling body weight and nest size we collected data in 68 non-experimental nests from four study years (2009–2012). We weighed nestlings to the nearest 0.25 g at the age of 7–9 d (1st day of age = the day of hatching). We analysed the relationship between nest size and nestling weight using general linear models in R 3.1.2 (R Core Team). The initial models comprised mean weight of nestlings in each nest as a response variable, and nest size, nestling age, brood size, nest social status, year, date, time of day when nestlings were weighed and male and female tarsus lengths as predictors. Model simplification was performed by backward stepwise elimination of non-significant terms from the initial model based on the change of deviance between the full and reduced models tested by a χ^2 test (Faraway 2006, Crawley 2007). We compared the levels of categorical predictors in the minimum adequate model using 'treatment' contrasts (Crawley 2007).

As in some parasitized nests the cuckoo eggs were either ejected or did not hatch and these nests consequently contained warbler nestlings, we used all successful nests regardless of brood parasitism (where at least one great reed warbler nestling fledged, n = 189) for testing the relationship between nest volume and offspring return rate (no fledgling from the nest returned in subsequent years = 0, at least one fledgling returned = 1). For the analysis we used Wilcoxon rank-sum test.

We also analysed the relationship between nestling body weight and experimental nest enlargement using all enlarged and control nests (for sample sizes see Table 1). The initial models comprised mean weight of nestlings in each nest as a response variable, and experimental treatment, nestling age, brood size, nest social status, year, date, time of day when nestlings were weighed and male and female tarsus length as predictors.

All subsets used for statistical analyses are summarized in Table 1.

Parental feeding effort

All analyses concerning parental feeding effort were performed using linear mixed-effects models (LMMs) implemented

Table 1. Subsets of nests used for statistical analyses (see Methods). In contrast to overall nest numbers, subsets used in statistical analyses comprise only one nest per female.

Analysis	Sample size	Nests in subset
Overall nest numbers		
–	643	All nests (329 individual females)
–	599	Measured nests (319 individual females)
Relationship between nest size and reproductive traits		
Nest size vs clutch size	209	Non-parasitized nests
Nest size vs brood size	165	Successful non-parasitized nests
Nest size vs nestling body weight	68	Non-manipulated nests with weighed nestlings
Nest size vs offspring return rate	182	Successful nests
Experimental nest size enlargement vs nestling body weight	29	Enlarged (n = 14) and control (n = 15) nests
Parental feeding effort		
Feeding effort vs nest size	18	Non-manipulated filmed nests
Feeding effort vs experimental nest size enlargement	29	Enlarged (n = 14) and control (n = 15) nests

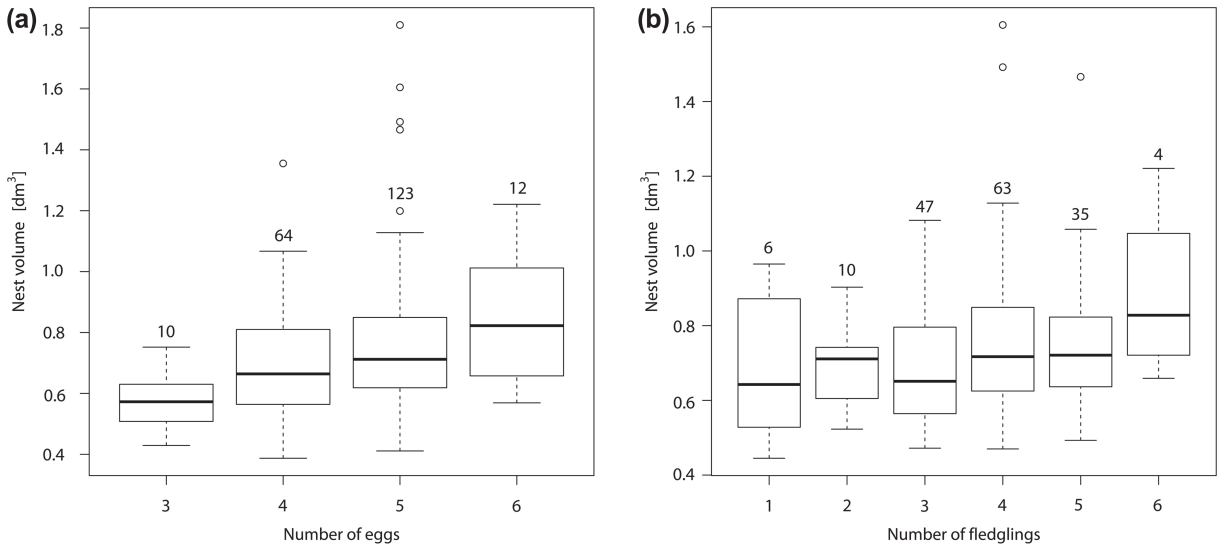

Figure 3. Volumes of great reed warbler nests with different clutch size (a) and brood size (b). Numbers above the boxplots represent the sample sizes for each category. The bottom and top of the box represent the first and third quartiles; the bold band inside the box is the median. The whiskers denote 1.5 of the interquartile range.

in the R package nlme (Pinheiro et al. 2015). In these models we fitted one random factor – nest identity – to account for the fact that both parents belong to the same nest. Model simplification was performed as described above. All continuous predictors were centred (Schielzeth 2010).

The role of nest size as the predictor of parental feeding effort was firstly explored in natural conditions on first monogamous nests from 2009 (n = 18). Initial models included amount of prey delivered to nestlings by male or female as a response variable, and nest volume, sex of parent, nestling age, brood size, date of filming and time of day when the filming started as predictors. To explore whether the feeding effort varied between sexes in different conditions (expressed by other predictors) we also added interactions between sex of parent and all other predictors into the model.

The initial models testing the effect of nest enlargement comprised amount of prey delivered to nestlings by the male or female as a response variable and treatment (enlarged or control), sex of parent, nestling age, brood size, nest social status, date of filming, time of day when the filming started, year (2011 or 2012) as predictors. We also included interactions between sex and all other explanatory variables in the model. We did not use pairwise comparison because of the desertion or predation of either enlarged or control nests. Nests with different social status were represented equally in both treatment (9 monogamous, 4 primary and 1 secondary nests in the enlarged group and 11 monogamous, 3 primary and 1 secondary nests in the control group). As only 3 (of 29 nests used in this analysis were first replacement nests, we did not use nest order as a predictor in our models.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.s60k4> (Jelínek et al. 2015b).

Results

Relationship between nest size and reproductive traits

We found a significant relationship between all four reproductive traits and nest size. Larger nests contained more eggs ($r_s = 0.23$, $p < 0.001$, n = 209, Fig. 3a) and nestlings ($r_s = 0.16$, $p = 0.035$, n = 165, Fig. 3b). Nestlings in larger nests had also higher body weight (Table 2a). Finally, fledglings from larger nests returned in subsequent years to our study area more frequently (W = 2633, p = 0.015, n = 182, fledglings returned from 53 nests).

Table 2. The effect of nest size (a), experimental nest size enlargement (b) and other predictors on the nestling body weight. If the nestling body weight did not differ between two categories of nests, they were pooled. Only the minimum adequate models are presented.

Model	Term	Estimate ± SE	t-value	p-value	DF	R^2
(a) Non-manipulated nests	Intercept	–5.57 ± 2.51			63	0.60
	Nest volume	4.91 ± 1.59	3.08	0.002		
	Age of nestlings	2.33 ± 0.30	7.54	< 0.001		
	Status-secondary*	–1.52 ± 0.59	–2.55	0.013		
	Time	0.34 ± 0.14	2.33	0.022		
(b) Enlargement experiment	Intercept	7.51 ± 5.47			27	0.12
	Age of nestlings	1.57 ± 0.71	2.20	0.036		

*Categorical predictors with two levels (reference category: monogamous and primary nests pooled).

Table 3. Table of the fixed effects from linear mixed-effects models analysing the amount of prey delivered to nestlings by parents in relation to nest size and experimental nest size enlargement. (a) Results of analyses of parental feeding in natural conditions (monogamous nests from 2009). (b) Results of the nest enlargement experiment. Only the minimum adequate models are presented. The significance of terms was assessed with type III analysis using Wald χ^2-test.

Model	Term	Estimate ± SE	χ^2	DF	p-value
(a) Non-manipulated nests	Brood size	11.34 ± 2.93	14.92	1	< 0.001
	Sex of parent*[a]	–12.01 ± 4.37	7.53	1	0.006
(b) Enlargement experiment	Treatment-enlarged*[b]	–6.89 ± 5.50	1.57	1	0.210
	Brood size	10.50 ± 2.77	14.32	1	< 0.001
	Sex of parent*[a]	–24.43 ± 4.94	1.39	1	0.237
	Time	–1.29 ± 1.41	0.84	1	0.358
	Treatment-enlarged*[b] × Sex of parent*[a]	17.85 ± 7.22	6.11	1	0.013
	Brood size × Sex of parent*[a]	–8.87 ± 3.64	5.94	1	0.014
	Time × Sex of parent*[a]	3.68 ± 1.85	3.92	1	0.047

*Categorical predictors with two levels (reference categories: female[a] and control nests[b]).

Nestling weight did not differ between enlarged and control nests (Table 2b).

Parental feeding effort

The observational data from 2009 showed that under natural conditions, nest size did not affect amount of prey delivered either by the male or female. The only variable which remained significant in the minimum adequate model was brood size (Table 3). The more nestlings were present in the nest, the more food both parents delivered, though males less than females (Fig. 4a).

The pattern of parental food supply, however, changed when we analyzed the effect of experimental nest enlargement (Table 3). While females still invested according to brood size (Fig. 4b), males responded to the manipulation and delivered significantly more food to the enlarged nests compared to the control ones (Fig. 5). Moreover, amount of food delivered by males surprisingly did not depend on brood size (Fig. 4b). Another important predictor of male feeding effort was time of recording. More specifically, the amount of food delivered by males increased during the day (Table 3).

Discussion

Maynard-Smith and Harper (2003) defined signal as 'any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved'. Thus, the fact whether any behavioural or visual characteristic serves as a signal or not depends on the existence of such a response. Apart from the role of nests in mate choice (Persson and Öhrström 1989, Evans and Burn 1996), their signalling function was also considered in association with the post-mating evaluation of male quality (Palomino et al. 1998, Soler et al. 1998a). By investing more time in nest building, males may signal their quality to females (Soler et al. 1998a). Correlations between nest size and various characteristics of male or female reproductive effort were found in several species (Møller 1982, Palomino et al. 1998, De Neve

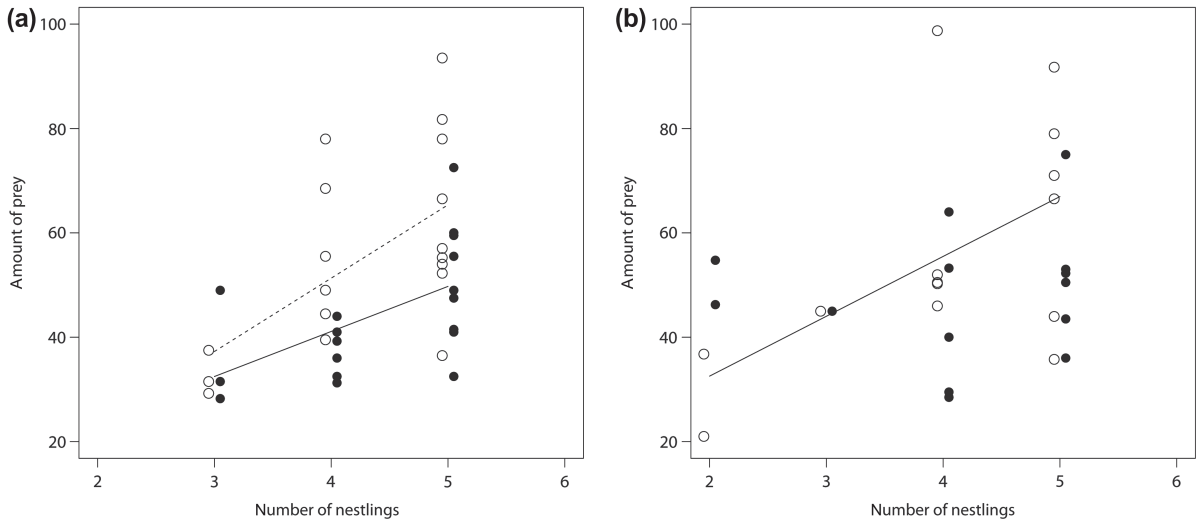

Figure 4. Male and female feeding efforts (expressed as amount of prey delivered during 3 h) in relation to brood size on (a) non-manipulated nests from 2009 and (b) experimentally enlarged nests from 2011 and 2012. Filled black circles and lines – males, open black circles and dashed lines – females. Lines indicate significant relationships based on simple regression models.

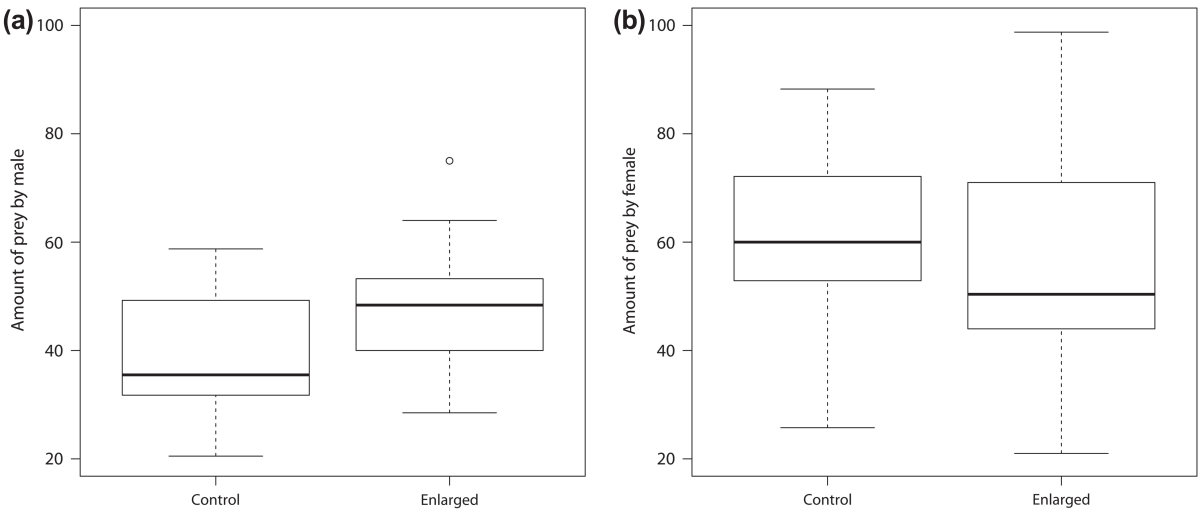

Figure 5. Boxplots depicting the amount of prey delivered by (a) male and (b) female during 3 h on experimentally enlarged (n = 14) and control (n = 15) great reed warblers nests. The bottom and top of the box represent the first and third quartiles; the bold band inside the box is the median. The whiskers denote 1.5 of the interquartile range.

and Soler 2002, Avilés et al. 2009, but see Antonov 2004, Lambrechts et al. 2012). Based on these pieces of evidence, however, one cannot distinguish whether nest size serves as a signal or is only a correlate of mate quality. The only two experimental studies examining the signalling function of nest size provided equivocal results (Soler et al. 2001, Tomás et al. 2013). Our study is the third evidence that size of avian nest could serve as a signal of mate quality. Specifically, we demonstrated that in the great reed warbler, where only females build the nests, males respond to the experimental enlargement of nest size by increasing the amount of food delivered to nestlings. They brought more food to their offspring in enlarged than in control nests, while females fed nestlings according to their number (Fig. 4b). The same positive relationship between brood size and amount of delivered food was found for both sexes in non-manipulated nests (Fig. 4a). This difference shows that males, contrary to females, changed their parental effort after the nest enlargement (Fig. 5). Females constructing larger nests can thus bring slightly less food to nestlings in response to increased feeding effort of their males. However, the difference between experimental and control nests in amount of food brought by females was not significant. In contrast to our study, Avilés et al. (2009) found that larger nests of the same species received more feedings per hour by both parents, which partially supported the sexual display hypothesis. Nonetheless, their study could be biased by short habituation and the fact that social status of the parents was unknown.

The discrepancy between the results of the experimental and correlative parts of our study may be caused by the fact that the range of nest sizes in non-manipulated nests was low and did not affect chick provisioning by males significantly. On the other hand, the design of our experiment emphasized the effect of nest size by enlarging the nests to the extent of the largest non-manipulated nests occurring in the population (Fig. 2). Only 33 of 599 nests measured between 2008 and 2012 were as large as our experimentally enlarged nests. Analogically, the function of blue-green egg coloration in post-mating female quality signalling (Moreno and Osorno 2003) was experimentally shown only in studies where artificial eggs on the edge of natural colour variation were used (Soler et al. 2008, English and Montgomerie 2011). Studies manipulating real eggs failed to find any relationship between the intensity of blue-green egg colour and male parental effort (Moreno et al. 2006a, Krist and Grim 2007, Johnsen et al. 2011) despite the extensive correlational and indirect evidence (Moreno et al. 2004, 2006b, López-Rull et al. 2007).

An inherent problem with all studies investigating post-mating signalling is the evaluation of individual quality, because its ultimate criterion, i.e. fitness, can be estimated only retrospectively and not accurately. The use of various body size criteria is problematic as well (Green 2001, Peig and Green 2010, Labocha and Hayes 2012). Thus, the estimation of an individual's quality in studies examining the role of nest size in post-mating signalling was frequently based on breeding success, ornament quality (male plumage chroma positively related to nest size, Broggi and Senar 2009), health state (not infected females built heavier nests, Tomás et al. 2006) or quality of immune response (nest material amount was positively related to immune response, Soler et al. 2007). A positive relationship between characteristics of parental quality and nest size was also found in great tits *Parus major*, (Álvarez and Barba 2008) and chinstrap penguins *Pygoscelis antarctica*, (Moreno et al. 1995). However, these relationships probably do not reflect mate quality signalling but result from differential allocation of resources in great tits (Broggi and Senar 2009) and better insulation properties of higher nests in chinstrap penguins (Fargallo et al. 2001). Nonetheless, we found similar relationships in the great reed warblers. Larger nests contained more eggs, more nestlings fledged from such nests and these nestlings were heavier. Finally, fledglings from larger nests had a higher return rate to our study site in subsequent years, which should be a correlate of fledgling survival and parental fitness. These findings together with the results of the experimental part give compelling evidence that nest size serves as a signal of female quality in the great reed warbler.

Given this result, one would expect that nestlings in experimentally enlarged nests should have higher weight (Table 2b) but this was not the case. This was probably caused by the fact that breeding success in the great reed warbler is primarily influenced by female effort (nesting attempt could be successful if only the female cares for nestlings but never when only the male cares – our unpublished results) and female quality represented by nest size was in both treatments the same (original nest size did not differ between the treatments, see Methods) which resulted in similar provisioning effort by females in both treatments. Thus, even the enhanced male feeding effort in enlarged nests did not significantly influence nestling weight.

Apart from birds, the use of extended phenotypes in post-mating signalling is limited. According to Maynard-Smith and Harper (2003), animal signals can be basically divided into 'indices', i.e. signals that are reliable because they cannot be faked, and 'handicaps', i.e. signals that are reliable because they are costly to produce. Many extended phenotypes with signalling function used by non-avian taxa are indices which carry information about presence or absence of an individual or its size (reviewed by Schaedelin and Taborsky 2009). Even though an index reflects the quality of the producer, such signal could be used mainly during mate choice, because it is known to a mate prior to mating like in the case of male-built nests in fishes (Barber et al. 2001). On the contrary, avian nests with signalling function are handicaps, and may be faked by a slightly increased building effort. Although nest building is costly by itself (Hansell 2000, Mainwaring and Hartley 2009), there could be other costs related to larger nests because only a small proportion of females build such nests (Fig. 2). In magpies, the additional cost of large nests probably lies in greater probability of parasitism by great spotted cuckoos *Clamator glandarius* which preferably parasitize larger nests belonging to parents of better quality (Soler et al. 1995). Our population of great reed warblers suffers from intensive parasitism by the common cuckoo, but a preference for larger nests was never found in this brood parasite neither in natural (Moskát and Honza 2000, Jelínek et al. 2014) nor in experimental conditions (Jelínek et al. 2015a). Nevertheless, larger nests could suffer from a greater predation pressure (Møller 1990, Biancucci and Martin 2010). Jelínek et al. (2015a) tested this assumption in enlarged and control great reed warbler nests (the same as in the present article) and found only marginally non-significant trend to higher predation of enlarged nests. Moreover, they used also dyads of large and small inactive great reed warbler nests and found no difference in predation rate between these two groups. Contrary to this, López-Iborra et al. (2004) showed that larger nests of great reed warblers baited with artificial eggs were more depredated than much smaller nests of reed warblers *Acrocephalus scirpaceus*. Thus, the evidence for higher risk of predation of larger nests in great reed warbler is rather equivocal and a selective pressure forcing great reed warbler females to build smaller inconspicuous nests could operate only in some site-specific conditions. For example at low predator densities nest predation could be affected rather by chance than by the inconspicuousness of a particular nest. This could be the reason of different results between studies López-Iborra et al. (2004) and Jelínek et al. (2015a) as the predation rate in the Spanish locality of López-Iborra et al. (2004) was much higher because almost all nests (97%) were depredated during short 14-d exposure while at the Czech site only 52% of nests were depredated within 30 d. Similarly, the evidence that larger active nests are more frequently depredated in other species is equivocal (Møller 1990, Palomino et al. 1998, Antonov 2004, Suárez et al. 2005).

We showed that females signal their quality after mating through nest size and thus influence the decision of their mates about how much to invest in the current brood. This signal was to date known primarily in males, however, we suppose that post-mating evaluation of the partner's quality is much more necessary in the sex which is not so choosy before mating. As females are the choosier sex, males would risk that they will end up with no reproductive output if they refuse the less attractive mates. When males pair with low-quality females, however, they can lower their parental investment according to the differential allocation hypothesis or concentrate on finding a second or higher quality females. According to this scenario, signalling greater willingness to invest into offspring should be more important for females and could be more widespread across animal taxa than previously assumed. A possible additional cost of enhanced probability of predation on large nests could cause that only superior great reed warbler females are willing to exhibit this trait to an excessive level.

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Supplementary material (Appendix JAV-00700 at <www.avianbiology.org/appendix/jav-00700>). Appendix 1.

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1

Nest size variability

- (2-3) – Size and material variability of great reed warbler nests

2

4

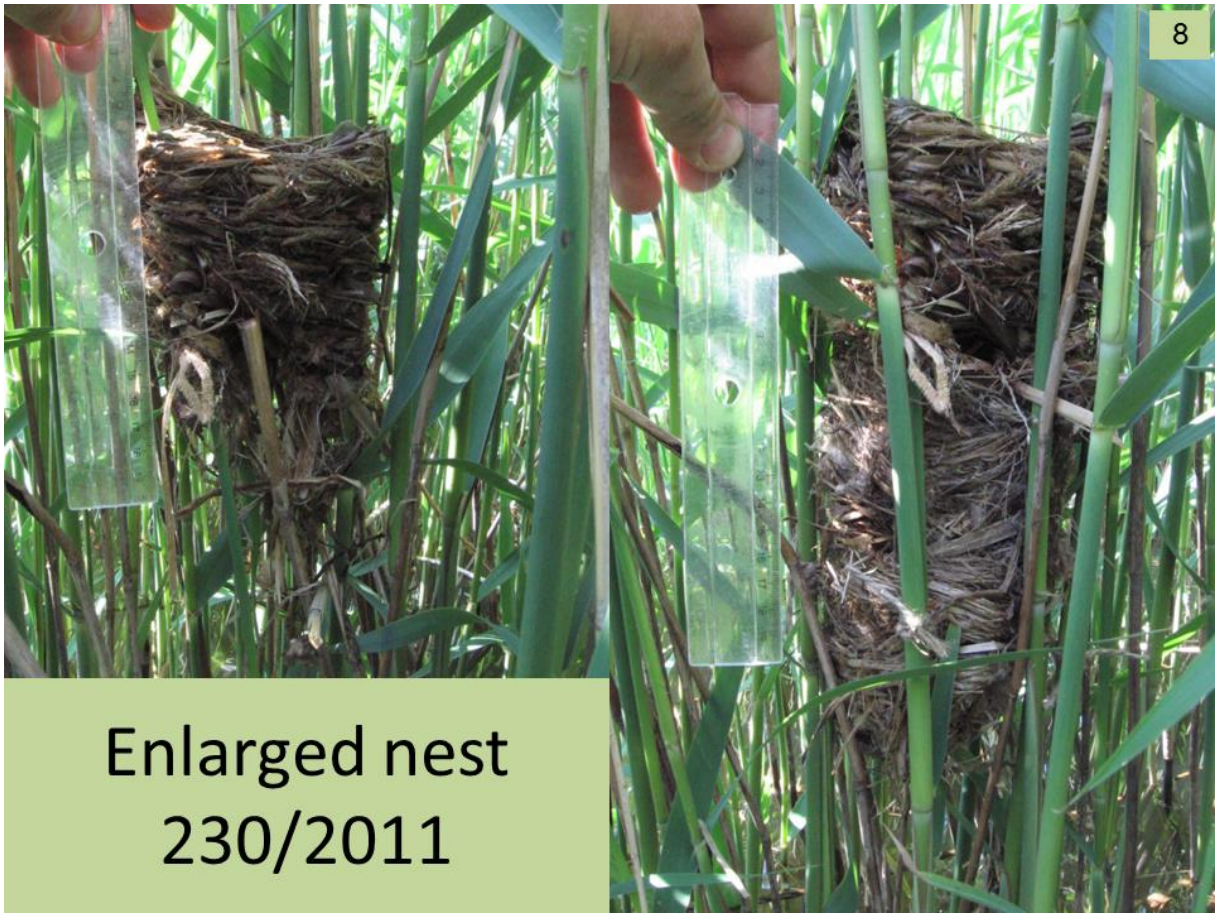
Enlargement experiment

- (5-9) – Some experimental nest before and after enlargement.


5
Enlarged nest
217/2011


6
Enlarged nest
514/2012


7
Enlarged nest
439/2012


8
Enlarged nest
230/2011

10

Enlargement experiment

- (11-15) – Comparison of sizes of enlarged nests and large unmanipulated nests


11
Natural nest 914/2012
Enlarged nest 514/2012


12
Natural nest 229/2009
Enlarged nest 103/2011


13
Natural nest 204/2013
Enlarged nest 424/2012


14
Natural nest 123/2008
Enlarged nest 524/2012

16

Enlargement experiment

- (17-18) – Photos of some control nests

17

Control nests:

102/2011 512/2011 214/2011

18

Control nests:

915/2012 536/2012 318/2012

Kapitola 5

Jelínek V. & Procházka P. (manuscript) Do females optimize nest cup size with respect to clutch size?

Opuštěné osmivaječné hnízdo rákosníka obecného (*Acrocephalus scirpaceus*). Rákosník obecný snáší za normálních okolností 2 až 5 vajec, jen výjimečně 6.

Do females optimize nest cup size with respect to clutch size?

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ABSTRACT

Nests are key structures for the reproduction of a majority of avian species. Thus, construction of a nest of proper quality in terms of mechanical support, inconspicuousness, thermoregulatory properties or providing enough space for eggs and nestlings constitutes an important component of successful reproduction. It has been hypothesised that bird females adjust the size of nest cups to their expected clutch size to ensure the best conditions for incubation of eggs and sufficient space for nestling development. We tested this hypothesis in an open cup nesting passerine, the great reed warbler (*Acrocephalus arundinaceus*), where the nest is built exclusively by the female. We found a positive relationship between clutch size and nest cup depth but not between clutch size and nest cup width – deeper but not wider nests accommodated larger clutches. We also found a positive relationship between nest cup size and nest width as well as female size. Nests built by the same female during the same year differed in their nest and nest cup dimensions – replacement nests being smaller than first nests. Finally, we found that the change in clutch size between first and replacement nests of the same female corresponds marginally significantly to the change in nest cup width but not to the change in nest cup depth. These results indicate that even though the design of the nest cup is determined also by other factors, such as female size or external nest size, great reed warbler females optimize nest cup dimensions for the particular clutch size. Future studies in different passerine species focusing on different nests built by the same females are necessary to confirm the general validity of this hypothesis.

KEYWORDS: nest cup dimensions, internal nest size, replacement clutch, female size, nest size, great reed warbler, replacement nest

SHORT TITLE: Nest cup size and clutch size

INTRODUCTION

Avian nests serve as receptacles for eggs and nestlings protecting them to a various extent against the environment and decreasing the incubation or heating costs of parents (Hansell 2000). This is especially the case in smaller birds – typically passerines which build narrower nests with deeper cups in comparison with larger birds where the nest is rather a platform (Deeming 2013). As the clutch represents progressively smaller proportion of bird's brood patch with increasing size of the bird, the thermoregulatory role of the nest becomes more important in smaller species (Deeming 2013). Deeper cups (Reid et al. 2002a, Windsor et al. 2013) or thicker nest walls (Whittow and Berger 1977, Skowron and Kern 1980) of smaller birds slow down the cooling rate of eggs and protect them against the wind especially in the presence of the incubating bird (Heenan and Seymour 2012).

It was experimentally shown that energy savings during incubation can be used during subsequent stages of the nesting cycle (Reid et al. 2000, Pérez et al. 2008) or even in subsequent breeding seasons (de Heij et al. 2006). Thus, it is not surprising that an increasing number of studies have shown that architecture of avian nests is well adapted to the environmental conditions. Populations breeding in colder environments (higher latitudes or altitudes) as well as individuals nesting earlier in the season when the temperature is lower, build nests with better insulating properties (reviewed by Heenan 2013). This can be achieved in various ways: nests can be larger (McCracken et al. 1997, Herranz et al. 2004), walls denser (Kern and Van Riper 1984, Franklin 1995) or lining layer thicker (Collias and Collias 1971, Mainwaring and Hartley 2008, Mainwaring et al. 2012).

Apart from these characteristics, thermal properties of nests are influenced by the selection of material, especially in nest cup lining (Slagsvold 1989a, Reid et al. 2002a, McGowan et al. 2004) and in the surface area of the nest cup (Heenan 2013). Narrower and deeper nest cups should lose heat less quickly as they shelter eggs against the wind which is considered to be more important for incubation energetics than conduction or evaporation (Webb and King 1983, Webster and Weathers 1988, Heenan 2013). Nonetheless, nest cups need not only provide the best environment for incubation of eggs but also for accommodation of nestlings during their growth. Too small nest cups can cause lower fledging success as Slagsvold (1982) experimentally showed in the Fieldfare (*Turdus pilaris*). During his experiment, nestlings frequently fell out of the nest when their number exceeded the number for which the nest cup was originally constructed. Moreover, crowded nests can suffer nestling mortality even in nest boxes as nestlings pushed out from the nest cup suffer suboptimal conditions (Slagsvold 1989a, Lombardo 1994).

These pieces of evidence suggest that it should be advantageous for birds to optimize the size of the nest cup for the particular clutch size (Snow 1978). If the nest cup is too large, incubation will be more costly in terms of energy expenditure and incubation length (Webb 1987, Reid et al. 2002b). If the nest cup is too small, it will not suffice to accommodate the nestlings even when the nest cup expands as the nestlings grow (Slagsvold 1989a). Indeed, some studies found a positive relationship between nest cup size and clutch size at interspecific (Slagsvold 1989b) or intraspecific level (Lombardo 1994, Álvarez and Barba 2008, but see Slagsvold 1982, Palomino et al. 1998, Herranz et al. 2005) indicating that females might adjust the cup size to the prospective clutch size. The fact that nest cups are built by females even in species where the other parts of nests are constructed solely by males (e.g. Collias and Collias 1971, Hoi et al. 1994) suggests that females have at least a good opportunity to fit the cup size to the number of eggs they are going to lay.

Unfortunately, the sole correlation between the cup size and clutch size does not reveal a female's intention to adjust the nest cup for a particular clutch size. Larger nest cups could be simply a consequence of the larger external size of whole nests. Similarly, larger nest cups accommodating larger clutches could be a consequence of female's size as bigger females can build larger nest cups

simply because they are bigger and use their bodies during the construction of the nest cup (Kluyver 1955, Hansell 2000) where they lay more eggs because they are also of better quality (because of their size, Labocha and Hayes 2012). If this is the case and nest cup size is the consequence of female size, each female should construct similar nest cups throughout her life regardless of the clutch or nest size.

Nonetheless, in all studies which have tested the relationship between nest cup size and clutch size, these possibilities were widely ignored probably because the authors did not know the identity of breeding females. Here, we coped with these problems and tested the clutch size hypothesis in the great reed warbler (*Acrocephalus arundinaceus*), an open-cup nesting passerine species. As we know the identity of almost all birds breeding in our study site, we were able to test not only the relationship between nest cup size and clutch size, female size or nest size, but also to compare nest cups of the same females across different breeding attempts both within and between breeding seasons.

METHODS

The study was conducted between 20 April and 31 July 2008-2012 in two adjacent fishpond areas between Hodonín (48º51′N 17º07′E) and Mutěnice (48º54′N 17º02′E) in South Moravia, Czech Republic. We systematically searched for nests in the littoral vegetation dominated by the common reed (*Phragmites australis*), with a smaller proportion of the narrow-leaved cattail (*Typha angustifolia*). Each nest was tagged with a small piece of coloured tape and its location recorded with GPS. Eggs were numbered using a felt-tip pen according to laying order to reveal missing eggs.

The population of great reed warblers numbering 80-100 pairs was systematically studied during the whole period. We caught males after their arrival and females during nest building, incubation or feeding of nestlings and marked them by a unique combination of standard aluminium ring and three plastic colour rings. Tarsus length, maximum wing length and weight of each caught bird were measured.

Nests and their dimensions

Great reed warblers build open-cup nests firmly tied to supporting reed stems (see supplementary material 1). Only the females are responsible for the whole nest construction (Kluyver 1955, see supplementary material 2 for an example of nest building). They build the nest structural layer out of dead plant material from previous years (especially reed or grass leaves and stalks) which they fish from water or wet in water just before they incorporate them in the nest (Kluyver 1955, Kožená-Toušková 1973, supplementary material 2). Thus, the nest typically becomes quite hard after it dries out. In contrast to the structural layer, the nest cup is built almost exclusively out of dry reed panicles.

We were able to find almost all nests each year thanks to regular mapping of male territories and checking for male mating status (Bensch 1996). Most nests were found during the building stage or at the beginning of egg-laying and were checked daily until clutch completion. Almost all nests were measured during the egg-laying period or incubation. Some nests were found later with large nestlings or had been destroyed by predators before measurements could be taken (from 3 to 9% per year). In these cases, we measured only those nest dimensions that remained intact. Nonetheless, all nests found after hatching were excluded from all analyses as nest cup expands during the nestling period (Slagsvold 1989a).

The following nest dimensions were recorded: nest height, nest width, nest cup depth, nest cup width, wall thickness and nest cup volume. Nest height was measured by callipers to the nearest mm from the nest rim to the bottom end of nest's structural layer ignoring the loose tags of nesting material by which great reed warbler nests usually terminates (see supplementary material 1). Nest width and nest cup width were measured by callipers to the nearest mm, nest cup depth was measured as a maximum distance from the nest cup bottom to its rim by a scaled stick (see supplementary material

1). Wall thickness was calculated as a half of a difference between nest and nest cup width. Apart from nest cup depth, all dimensions were obtained as the mean of two independent measurements. Nest cup volume (V) was calculated as half an ellipsoid according to the formula: $V = {}^{4}/_{3}\left(\pi \times a^{2} \times b \times {}^{1}/_{2}\right)$ where a = nest cup radius and b = nest cup depth (Møller 1982). All nests were measured by one person (VJ).

Great reed warblers build a new nest for almost each nesting attempt (only in 2 of 131 cases, the female laid a replacement clutch into the same nest as her first clutch) giving us an opportunity to test the relationship between nest cup dimensions of different nests of the same female across one breeding season. For this reason, we classified nests of the same female as first, first replacement, second replacement nest etc. according its order during the season. For all statistical analyses we used only the first replacement nests (hereafter "replacement nests") in order to make all replacement nests comparable. As unsuccessful females sometimes divorce and abandon their first breeding territory trying to find another appropriate place where to breed, we found several females arriving at our study site unusually late in the season (from mid-June). As these late-arriving females almost certainly have already bred elsewhere, we excluded their nests from all analyses as the exact order of their nests is unknown.

Clutch size

Great reed warblers are regularly parasitized by the common cuckoo (*Cuculus canorus*) at our study site (up to 50 % of nests, for details see Jelínek et al. 2014). Cuckoo females locate host nests mostly during nest building and subsequently lay their eggs into host nests (Wyllie 1981). Before or during egg-laying, they successively remove up to four host eggs (Gärtner 1981) lowering host clutch size even in cases when these eject the parasitic egg. Moreover, the common cuckoo is also a nest predator and it frequently partially (Moksnes et al. 2000) or exceptionally completely (Davies 2000) depredates host clutches. For these reasons, we consider as parasitized each nest where we recorded a parasitic egg or missing host eggs in laying sequence. As usual clutch size of first great reed warbler nests ranges from four to six eggs (our unpublished results), we consider as parasitized also those nests found with unusually low number of eggs (two or three) in May and the first half of June (natural two- or three-egg clutches appear from the second half of June and especially during late breeding attempts in July, our unpublished results). The rest of great reed warbler nests were classified as non-parasitized. As we could not be sure that we had recorded exact clutch size in parasitized nests, we excluded these nests from analyses concerning clutch size.

Selection of variables

In a first step of the statistical analyses, we examined the relationships among three variables characterizing the size of the nest cup. We found a strong correlation between volume and width or depth of the nest cup (r_p = 0.80 and 0.52, N = 171) which is logical as nest cup volume is calculated from these two variables. However, we found no correlation between nest cup width and depth (r_p = -0.02, N = 171). For these reasons and because nest cup width and depth could have different importance in nest architecture, we used them both as response variables and performed all analyses for each of the two variables separately.

To characterise female size, we used tarsus length. We suppose that this measurement should be the most important in nest cup building process as the female moulds the nest cup by pushing its belly and chest against the nest wall while using typical movements by the legs to tamp down and compact the material (see Kluyver 1955 and supplementary material 2). Moreover, tarsus length does not change between years in great reed warblers (comparison of birds measured during two subsequent years in 2008-2012, paired t-test: t = 0.34, p = 0.74, N = 220) as well as in other bird species (Smith et

al. 1986, Verhulst et al. 2014) which is very important as we were not able to catch all females each year. These females were identified by their colour ring combinations and in such cases we used measurements from previous years. We did not use wing length as great reed warblers undergo their complete moult each winter and wing length can reflect rather environmental conditions on their wintering grounds than bird's actual size. Moreover, many great reed warblers arrive with their primaries already abraded making determination of an accurate wing length difficult. We could not use weight because we caught females at different stages of the breeding cycle and this parameter dramatically differs e.g. when a female is about to lay an egg or when she is provisioning her offspring.

External nest dimensions could also influence the size of nest cups as wider nests can accommodate wider cups and higher nests deeper cups. Thus, we used wall thickness, nest width and nest height to characterise nest size. Unfortunately, a strong positive correlation between nest width and wall thickness ($r_p = 0.79$, N = 171) prevented us from using them simultaneously in one model. For this reason, we used only nest width as a predictor of nest cup width.

Statistical analysis

For the analyses explaining the relationships between nest cup dimensions and clutch size, external nest size and female size, we used only first (not replacement) non-parasitized nests with intact nest cups where females started to lay eggs before 16th June as new females who arrived at our study site after this date had probably already bred elsewhere. Clutches with less than four eggs are extremely rare in first great reed warbler nests at our study site and we cannot be sure whether this small number of eggs in a clutch is natural or a consequence of unnoticed brood parasitism by the common cuckoo. Thus, we excluded five nests with three-egg clutches from our analyses. We used general linear models for statistical analyses. We did not use the mixed modelling approach as our dataset would be very unbalanced (33 females with more than one nest vs. 138 females with only one nest). Thus, we randomly chose one nest for each of these 33 females with two or more nests from different years (final dataset contained 171 nests). We present full models containing all predictor variables that were a priori deemed important. The model for nest cup width included clutch size, female tarsus length, wall thickness as predictors and laying date of the first egg (1 May = day 1) and year (nominal variable) as covariates. The model for nest cup depth included clutch size, female tarsus length and nest height as predictors and laying date and year as covariates. There was no strong correlation among the explaining variables and covariates (all $r_s < 0.36$).

To eliminate the effect of female size on nest cup size or clutch size, we compared nest cup size of first and replacement nests with intact nest cups constructed by the same female. Firstly, we used those pairs of the first and replacement nests built during the same breeding season (78 pairs of nests). Nine females had two pairs of nests from different breeding seasons in the dataset. Thus, we randomly excluded one pair of nests for each of these nine females to avoid temporal pseudoreplications (Hurlbert 1984). The overall dataset contained 69 pairs of nests. As all variables complied with normality, we used paired t-tests to test the differences in nest and nest cup dimensions between the first and replacement nests.

Secondly, as clutch size is substantially influenced by brood parasitism (see above) we had to further reduce the dataset to 23 pairs of first and replacement nests for the comparison of clutch sizes. To test the difference in clutch size, we used paired Wilcoxon signed rank test.

Thirdly, because 14 of these 23 pairs of nests differed in clutch size (one egg less in replacement nest), while in the remaining 9 nests there were the same numbers of eggs in both nesting attempts, we were able to test whether the change in nest and nest cup dimensions between first and replacement nests built by the same female during the same year corresponds to the change in clutch

size. As all variables (calculated as a particular dimension of the first nest minus the same dimension of the replacement nest) complied with normality, we used parametric t-tests.

Finally, we intended to test whether nest cups of the first nests of the same female constructed in different years differ in response to the difference in clutch size or nest size. Nonetheless, only 5 of 38 suitable pairs of nests differed in clutch size precluding further statistical analysis.

All statistical calculations were performed in R 3.1.2 (R Core Team 2014).

RESULTS

Both nest cup dimensions were significantly influenced by female tarsus length – bigger females built wider and deeper nest cups; however, the influence of clutch size and nest size on nest cup size differed between the two nest cup dimensions (Table 1). While clutch size explained a significant proportion of variability in nest cup depth, there was no such a relationship in nest cup width. A different relationship was also found for nest size dimensions as nest cup width was significantly influenced by nest width; however, nest height did not influence nest cup depth (Table 1).

Replacement nests were significantly lower (paired t-test: $t = 3.18$, $N = 68$, $P = 0.002$, Fig. 1) and narrower ($t = 3.67$, $N = 68$, $P < 0.001$, Fig. 1), their nest cups were significantly shallower ($t = 4.08$, $N = 67$, $P < 0.001$, Fig. 1) and narrower ($t = 2.13$, $N = 69$, $P = 0.036$, Fig. 1), but their walls were not significantly thinner ($t = 1.83$, $N = 67$, $P = 0.071$) compared with first nests of the same females. Replacement nests had significantly smaller clutch sizes (first clutch ± SE = 4.9 ± 0.1 eggs, replacement clutch = 4.3 ± 0.1 eggs, paired Wilcoxon signed rank test: $V = 112.5$, $N = 23$, $P = 0.001$).

Only the change in nest cup width between first and replacement nests differed marginally significantly between pairs of nests with the same and different clutch size (t-test: $t = -2.08$, $P = 0.053$). This means that when the replacement nest had lower clutch size than the first nest, it had also narrower nest cup, while nest cup width did not differ between first and replacement nests with the same clutch size (Fig.2). Other variables did not differ significantly between the two nest categories: change in nest cup depth ($t = 0.95$, $P = 0.35$), wall thickness ($t = 1.65$, $P = 0.12$), nest width ($t = 0.25$, $P = 0.79$) and nest height ($t = 0.79$, $P = 0.43$).

DISCUSSION

In our study, we tested the hypothesis that great reed warbler females adjust the size of their nest cups to their expected clutch size to secure the most appropriate environment for eggs during incubation and enough space for nestlings during their growth. For first (non-replacement) nests of each female, we found that (i) while nest cup width was unaffected by clutch size, nest cup depth was positively related to clutch size. In contrast to that, (ii) only nest cup width was affected by the respective nest dimension: wider nests accommodated wider cups but there was no relationship between nest height and nest cup depth. Finally, (iii) both dimensions were significantly positively affected by female size expressed as tarsus length. For replacement nests, we found that (iv) they were smaller and had smaller nest cups than first nests even when we compared nests built by the same female during the same year and (v) that the change in clutch size between first and replacement nests of the same female corresponds marginally significantly to the change in nest cup width but not to the change in nest cup depth.

Although our correlative approach cannot effectively test for causal mechanisms, our results suggest that the design of great reed warbler nest cups is affected by several factors as indicated by different results for nest cup width and depth. Larger females build wider and deeper nest cups showing that the nest cup construction is significantly affected by the size of the building bird.

Nonetheless, female body size is not the only driver of nest cup size as supported by the results of our second analysis where replacement nests had significantly narrower and shallower nest cups than first nests constructed by the same female during the same year. It must be pointed out that the smaller nest cup size of replacement nests could be and probably is driven also by other factors. It is especially the greater haste during the building of replacement nests which could influence nest cup dimensions as we found significant differences also between external nest dimensions of the first and replacement nests (also De Neve and Soler 2002) – smaller nest cups were built in smaller first replacement nests. Other factors, such as different nest material composition, could hardly influence nest and nest cup dimensions as nest material is well accessible in great reed warbler territories or in their close vicinity throughout the season and we did not notice any difference in the nest material composition between the first and replacement nests.

The relationship between nest cup size and female size can be driven by at least two mechanisms. The first rests in a direct mechanical influence of female size during shaping the nest structural layer surrounding the nest cup and the nest cup itself as she pushes its belly and chest against the nest wall quite heavily during nest and especially nest cup construction resulting in very solid nest cups frequently enduring the entire nesting cycle without a substantial change (our observations, see supplementary material 2). The second, indirect mechanism is driven by the fact that bigger females can also lay more eggs and construct accordingly larger nest cups. Nonetheless, only nest cup depth but not width was affected by clutch size. This difference between the results for nest cup width and depth can be caused by the spatial constraints of great reed warbler nest sites. While nest cup depth can be theoretically almost unlimited as females can build nests as high as they want (see supplementary material 1), nest width is probably more influenced by the position of supporting reed stems. Moreover, as nest wall provides thermoregulatory properties of the nest (Whittow and Berger 1977), its thickness together with external width of the nest should also influence nest cup dimensions. If nest width is to some extent constrained by distance between supporting reed stems, the change in nest wall thickness has to be at the expense of nest cup width. Indeed, our data showed that nest width together with nest wall thickness (which are strongly positively correlated, $r_p = 0.79$) significantly negatively affected the width of nest cup. Thus, wider nests have thicker walls manifesting in narrower nest cups (correlation between nest cup width and wall thickness: $r_p = -0.36$, $P < 0.001$) suggesting that nest wall thickness could be of greater importance than nest cup dimensions.

Although common cuckoo parasitism and nest predation are the most detrimental factors influencing the survival of great reed warbler nests (of 298 unsuccessful nests, 90 nests were depredated and 110 failed due brood parasitism during the five years of this study), heavy and especially long-lasting rains and storms with strong winds could also importantly influence the breeding success of this species. During these events, some reed beds become flattened and if the nest is placed in that part of the reed bed it gets into a very inappropriate position for successful nesting. For that reason, the nest cup depth could be of special importance in such circumstances as smaller nestlings and especially eggs can fall out of these nests. However, we recorded only six nesting attempts which failed due to flattening of the reed stands during the 2008-2012 breeding seasons. From these pieces of evidence, we are convinced that if the particular reed bed does not completely flatten and the nests do not end up in a horizontal position all great reed warbler nests are sufficiently deep to prevent eggs or smaller nestlings from falling out. This is probably caused also by the fact that great reed warbler females are capable of incubating eggs or brooding nestlings even in this harsh weather conditions which prevent eggs or nestlings from falling out of the nest. Such behaviour is probably very demanding also during long-lasting rains as females can leave nests less frequently if at all. For example, during a long rainy period in May 2008 two nests were deserted by females, however, they both had immediately started to build replacement nests. This suggests that the almost

continual incubation during harsh weather conditions could be more energetically demanding than building a new nest, laying replacement clutch and its subsequent incubation. Hence, construction of nest cup of proper size and thermoregulatory properties could be even more important in rainy periods than in still weather which is in accordance with our hypothesis.

The evidence for validity of the clutch size hypothesis in other species is equivocal and comprised only analyses of the relationship between clutch size and various nest cup dimensions without the possible influence of nest width or wall thickness. This is important primarily in open cup nesting birds where nest architecture often depends on nest site and whose nests are more exposed to weather conditions. Therefore, in contrast to cavity nesters, they can react on the environmental conditions by adjusting the external nest dimensions (Mainwaring et al. 2014) which could also influence the size of the nest cup. For example, Herranz et al. (2005) found no relationship between cup size and clutch size but found a negative correlation between laying date and wall thickness in the skylark (*Alauda arvensis*) and the short-toed lark (*Calandrella brachydactyla*). Thus, a stronger selection on the better insulating nests early in the season could override the relationship between clutch size and nest size. Similarly, Palomino et al. (1998) testing the clutch size hypothesis in another open nester – the rufous-tailed scrub robin (*Cercotrichas galactotes*) found no relationship between nest cup volume and clutch size. However, they measured nest cup dimensions after termination of each nesting attempt and thus nest cup volume could be more related to brood size than to clutch size due to the nest cup expansion by the activity of nestlings (Slagsvold 1989a).

The situation in cavity nesters is different as the size and shape of their nests and consequently the size of nest cups is constrained by cavity size especially in small natural holes. On the other hand, artificial nest boxes where the secondary cavity nesters are mostly studied are generally larger than natural holes (Wesołowski 2003). Consequently, the lower part of the nest box is almost always filled with nesting material regardless of nest box size (Deeming 2013) enabling construction of nest cups of proper size. Indeed, Álvarez and Barba (2008) found a positive relationship between nest cup size and clutch size in great tits (*Parus major*) which is in accordance with the finding of Møller et al. (2014) who showed a positive relationship between cavity size and clutch size in this species.

An experimental test of the clutch size hypothesis is probably almost impossible as it would have to comprise the change of a complete nest before the initiation of egg-laying. As females frequently tune nest cup shape even after the nest is seemingly complete (by adding material into the lining layer or shaping the nest cup), it is hard to imagine that they would accept such a treatment. To resolve this problem, we used a natural experiment where we compared change in nest cup dimensions between first and replacement nests (constructed by the same female) between pairs of nests where the clutch size decreased by one egg and pairs of nests where the clutch size remained the same. If the clutch size hypothesis is valid, this change should be greater in the group of nest pairs with decreased clutch size than in group of nest pairs with the same clutch size. We found this relationship only for nest cup width indicating that females build narrower nest cups for smaller replacement clutches. However, the result of the statistical test was marginally significant.

To sum up, even though Slagsvold (1989b) found a positive relationship between clutch size and nest cup size on the interspecific level, very few studies tested this relationship on the intraspecific level. This is mainly because researchers primarily focused on external nest dimensions widely ignoring nest cup as an important nest feature. Future studies should aim at species with variable clutch size and with high nest site fidelity to test the relationship between clutch size and cup size of nests built by the same female within and between seasons.

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CONFLICT OF INTEREST

We declare that both authors have no conflict of interest.

ETHICAL STANDARDS

The study complies with the current laws of the Czech Republic.

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Table 1: The effect of clutch size, female size and nest size on the nest cup dimensions (width and depth) in first non-parasitized great reed warbler nests. Full models with adjusted R^2 are presented. Reference level for variable year is 2008. Statistically significant p-values are highlighted in bold.

Nest cup width (R^2 = 0.19)			
	Estimate ± SE	t	P
Intercept	15.81 ± 10.27	1.53	0.126
Clutch size	0.24 ± 0.53	0.45	0.650
Female tarsus length	1.25 ± 0.36	3.46	< **0.001**
Nest width	0.17 ± 0.04	3.54	< **0.001**
Laying date	0.06 ± 0.03	1.88	0.061
Year 2009	0.28 ± 0.70	0.40	0.683
Year 2010	2.68 ± 0.83	3.19	**0.002**
Year 2011	1.11 ± 0.81	1.36	0.175
Year 2012	1.89 ± 0.83	2.27	**0.024**
Nest cup depth (R^2 = 0.20)			
	Estimate ± SE	t	P
Intercept	33.88 ± 12.91	2.62	0.010
Clutch size	1.77 ± 0.64	2.73	**0.007**
Female tarsus length	0.88 ± 0.44	1.99	**0.048**
Nest height	0.00 ± 0.01	0.21	0.831
Laying date	-0.052± 0.04	-1.21	0.226
Year 2009	-0.41 ± 0.85	-0.48	0.627
Year 2010	-4.98 ± 1.02	-4.87	< **0.001**
Year 2011	-0.82 ± 0.98	-0.83	0.404
Year 2012	-0.56 ± 1.03	-0.54	0.586

502 **Fig. 1:** Comparison of nest and nest cup dimensions of 69 pairs of first and first replacement great
503 reed warbler nests (in mm). The bottom and top of the box represent the first and third quartiles; the
504 bold band inside the box is the median. The whiskers denote the lowest or highest values up to 1.5 of
505 the interquartile range and dots depict outliers.

506

507 **Fig. 2:** Difference of nest cup width (in mm) in 9 pairs of first and first replacement great reed warbler
508 nests where the clutch size remained the same and 14 pairs of nests where the clutch size decreased by
509 one egg. The bottom and top of the box represent the first and third quartiles; the bold band inside the
510 box is the median. The whiskers denote the lowest or highest values up to 1.5 of the interquartile
511 range.

512

Supplementary material 1. Examples of some great reed warbler nests and specification of nest cup depth and nest height measurement techniques.

Supplementary material 2. A video recording exemplifying nest construction by a female great reed warbler.

Figure 1

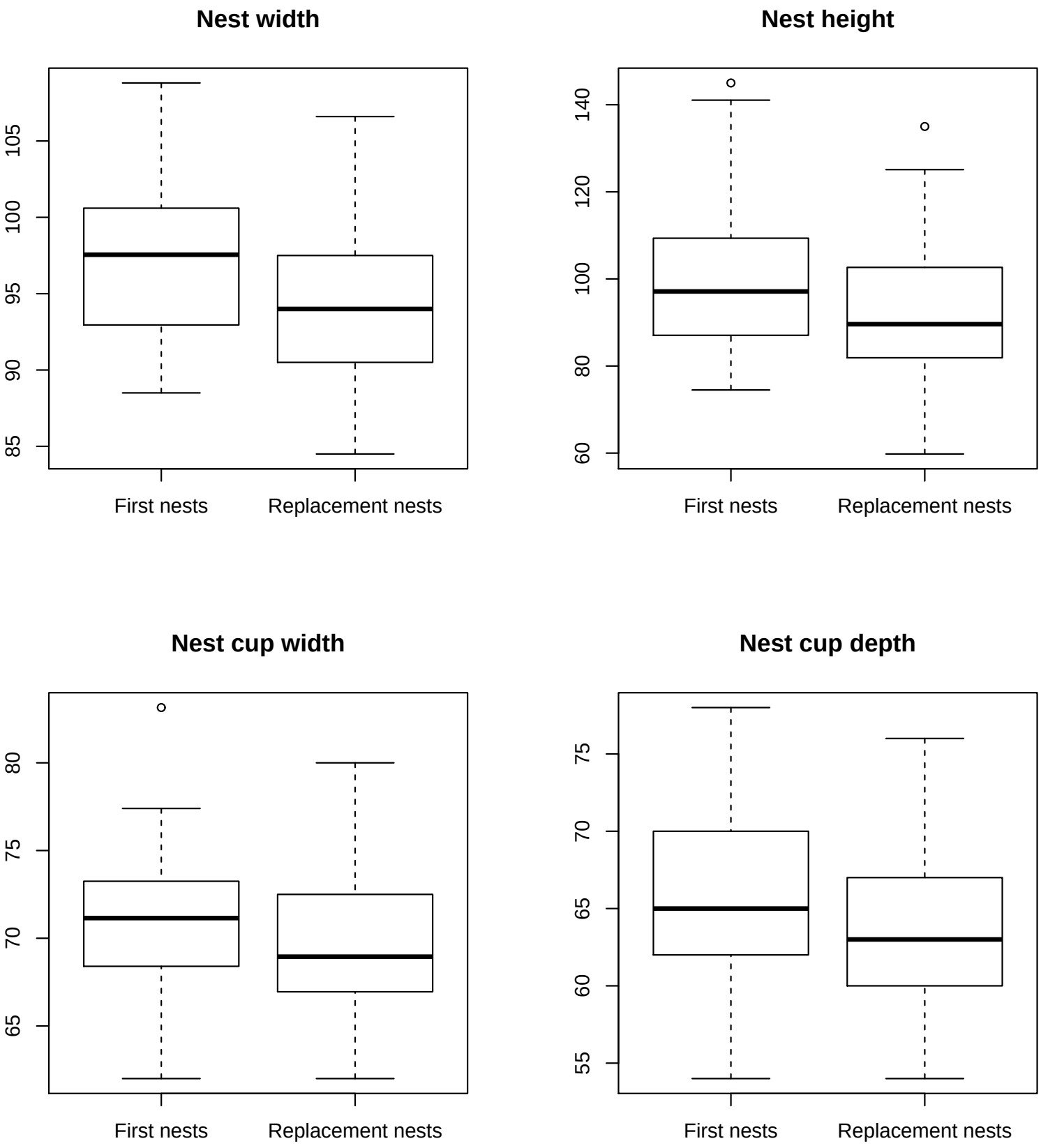
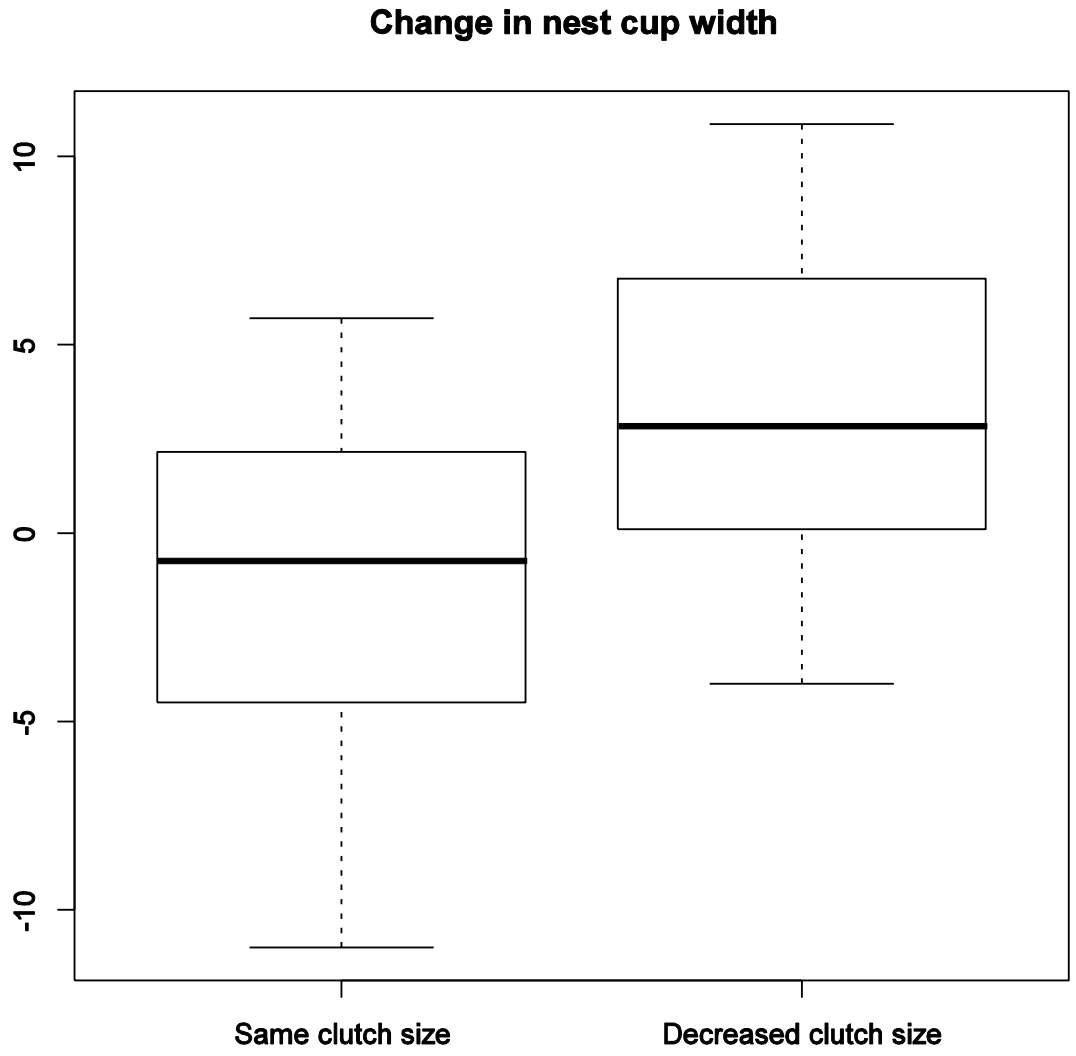

Nest width
85
90
95
100
105
First nests
Replacement nests
Nest height
60
80
100
120
140
First nests
Replacement nests
Nest cup width
65
70
75
80
First nests
Replacement nests
Nest cup depth
55
60
65
70
75
First nests
Replacement nests

Figure 2

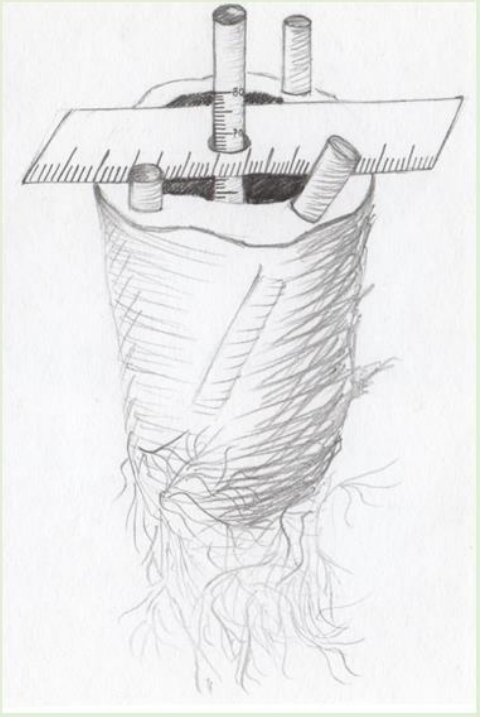

Change in nest cup width
10
5
0
-5
-10
Same clutch size
Decreased clutch size

Supplementary material 1

Examples of great reed warbler nests

Examples of great reed warbler nest cups.

Nest cup depth measurement



Nest height measurement